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THE ARCTIC-ALPINE ELEMENT OF THE VASCULAR FLORA AT LAKE SUPERIOR

David R. Given

and

James H. Soper

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Abstract

A study of the occurrence of arctic-alpine vascular plants around the shores of Lake Superior has found greatest concentrations at several sites on the north shore from Pigeon River to Pic River, with secondary centres in two canyons inland from Thunder Bay, around Lake Nipigon, near Wawa, on Michipicoten Island and the Keweenaw Peninsula of Michigan. Forty-eight species are accepted as constituting an arctic-alpine element and their distribution and habitats are described. Plant communities containing arctic-alpine species are classified into thirteen groups within five classes. It is suggested that arctic-alpine plants have persisted at Lake Superior since the time of the receding Wisconsin ice-sheet when vegetation of an arctic-subarctic character was more widespread in areas south of the Laurentide ice sheet. Subsequent development of the boreal coniferous forest and the expanse of acidic granite-derived soils prevented their migration or caused their disappearance in the region between Lake Superior and Hudson Bay. The chief factors proposed for maintaining arctic-alpine habitats in the area are stress and (to a lesser degree) disturbance. The harsh microclimate of exposed parts of the shoreline is a major factor, including the direct effects of snow and ice, low summer temperatures and fogs.

Résumé

Cette étude porte sur les plantes vasculaires de la région située autour du lac Supérieur. Ces plantes démontrent une affinité arctique-alpine. On en a noté des concentrations importantes à plusieurs endroits sur la rive nord du lac entre les rivières Pigeon et Pic. Il y a aussi des sites secondaires dans deux cañons à l'intérieur des terres soit au nord-est de Thunder Bay, autour du lac Nipigon, près de Wawa, ainsi que dans l'île Michipicoten et dans la péninsule de Keweenaw, Michigan. On définit un élément arctique-alpin composé de 48 espèces en plus de décrire leur répartition et leurs habitats. Les communautés végétales qui contiennent des espèces arctiques-alpines sont réparties en 13 groupes formant cinq classes. On croit que ces plantes auraient persisté autour du lac Supérieur depuis le retrait de la calotte glaciaire du Wisconsin alors que la végétation à caractère plus ou moins arctique était largement répandue dans les régions au sud de la calotte glaciaire Laurentide. Le développement subséquent d'une forêt coniférienne et l'étendue des sols acides entre le lac Supérieur et la baie d'Hudson auraient prévenu la migration des espèces arctiques-alpines ou en auraient causé la disparition. Les facteurs principaux qui pourraient expliquer le maintien des communautés arctiques-alpines dans cette région sont la compétition et, à un moindre degré, la perturbation. Le microclimat rigoureux des sections côtières exposées aux forces climatiques constitue un facteur important, y compris les effets directs de la neige et de la glace en hiver d'une part, et d'autre part des températures plus basses en été, souvent accompagnées de brumes épaisses.

INTRODUCTION

The occurrence of arctic-alpine plants at relatively low latitudes is a phenomenon of considerable interest to phytogeographers, ecologists, geologists and others concerned with patterns of glacial retreat, climatic change and the history of associated development of vegetation. Apart from exhibiting patterns of disjunct distribution which demand explanation, such occurrences often provide clues to possible pathways for the post-glacial migration of plants and to past patterns of vegetation in areas of tundra along ice-margins. Aggregations of assemblages of disjunct arctic-alpine species in particular localities may indicate local microclimates quite different from the general climate of the region.

Extensive botanizing since the early nineteenth century has established that the Lake Superior drainage basin, including parts of Ontario, Michigan, Wisconsin and Minnesota, is rich in arctic-alpine plants. Greatest concentrations occur along the rocky shores of the lake as an intermittent treeless strip of tundra-like vegetation, but similar communities are also found occasionally away from the lake at topographically unusual sites where the development of forest is inhibited. The nearest continuous arctic tundra is at James Bay, several hundred kilometres to the northeast. Some of the species occurring at Lake Superior display spectacular disjunctions between their main areas of distribution in the Arctic and localities one thousand kilometres or more to the south around Lake Superior and at other low latitude sites. Although as early as 1848 Louis Agassiz was impressed with the tundra-like communities frequently encountered along the Lake Superior shore (Agassiz, 1850), the published documentation of the regional flora is conspicuously meagre. Arctic-alpine species have been mentioned in passing by numerous authors but the only detailed accounts of the communities are those published for Old Woman Bay (Soper & Maycock, 1963) and the northern part of Cook County, Minnesota (Butters & Abbe, 1953). However, several lists of species and brief accounts of the vegetation have been published by others (Fernald, 1935; Hosie, 1938; Brown, 1937; Schuster, 1957, 1958a, 1958b).

HISTORICAL BACKGROUND

The beginnings of botanical observations in the Lake Superior region can be traced to early explorations which were carried out well over one hundred and fifty years ago. A detailed review of the activities of the pioneering explorers in the Upper Great Lakes region during the nineteenth century has already been presented by E.G. Voss (1978). We have selected from that period only a few names of persons whose discoveries seem relevant to the recognition of the arctic-alpine element in the flora.

In 1831 Dr. Douglass Houghton (1809-1845) acted as the naturalist on an expedition which travelled by canoe from Sault Ste. Marie along the south shore of Lake Superior, returning about ten weeks later. He collected *Empetrum nigrum* at the Picture Rocks and sent many of his specimens to John Torry for verification (Figure 1, Loc. 40).

The collections and observations made by Louis Agassiz (1897-1873) were the first to focus attention on the arctic-alpine plants around the shores of Lake Superior. With a party of Harvard students and others, Agassiz made a canoe trip in the summer of 1848 from Sault Ste. Marie to Thunder Bay where he penetrated the Kaministiquia River as far as Kakabeka Falls and then returned to the Sault. Because of previous familiarity with vegetation above timberline in the Swiss Alps, Agassiz was struck by the similarity between the tundra-like habitats along the north shore of Lake Superior and alpine habitats he had known in Europe. In his report on the flora (Agassiz, 1850), there are lists of vascular plants which include ten of the commonest arctic-alpine species at Lake Superior. His record for *Loiseleuria procumbens* is the only artic-alpine species which remains unsubstantiated by a

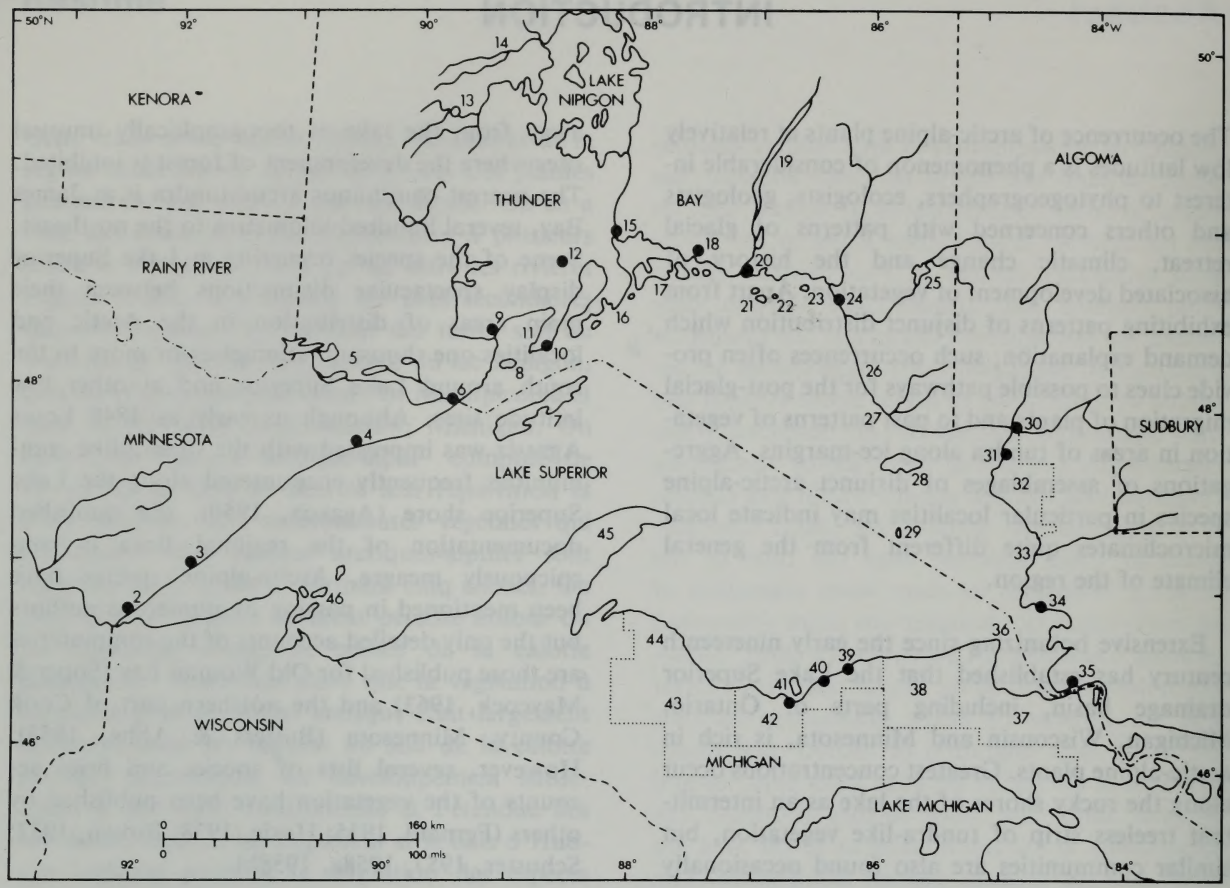

Fig. 1. Chief localities mentioned in the text.

1. St. Louis River
2. Duluth
3. Two Harbors
4. Grand Marais
5. Border Lakes
6. Pigeon River
7. Isle Royale
8. Pie Island
9. Thunder Bay
10. Silver Islet
11. Sibley Peninsula
12. Ouimet Canyon - Cavern Lake
13. Garden Lake
14. Obonga Lake
15. Nipigon
16. Black Bay Peninsula
17. St. Ignace Island
18. Rossport
19. Longlac
20. Terrace Bay
21. Slate Islands
22. Leadman Islands
23. Pic Islands and McDonalds Islands
24. Pic River - Heron Bay
25. White Lake
26. Pukaskwa National Park
27. Pukaskwa River
28. Michipicoten Island
29. Caribou Island
30. Wawa - Michipicoten Harbour
31. Old Woman Bay
32. Lake Superior Provincial Park
33. Montreal River
34. Batchawana Bay
35. Sault Ste. Marie
36. Whitefish Point
37. Chippewa County
38. Luce County
39. Grand Sable Dunes
40. Pictured Rocks
41. Munising
42. Alger County
43. Marquette County
44. Huron Mountains
45. Keweenaw Peninsula
46. Apostle Islands

specimen or by rediscovery since his trip. We suspect that this report was based on a misidentification, probably a sterile specimen of *Empetrum nigrum*. A similar explanation has been proposed for a report of the same species from the south shore of the lake (see Voss, 1978, footnote 233, p. 60). It is unfortunate that Agassiz did not give specific collection sites in his published list nor on the labels of his specimens (cited only as from "L. Superior" on those which we have seen).

Robert Bell, attached to the Geological Survey of Canada, assisted in the summer of 1860 on an exploration along the east and south shores of Lake Superior. Bell's collections from the expedition (Bell, 1861) and from a later one up the

Michipicoten River and across the height of land into the Moose River drainage basin were included by John Macoun in his Catalogue of Canadian Plants (Macoun, 1883-1890).

An American surveyor, O.B. Wheeler (1835-1896), who worked as part of a triangulation team on American and Canadian portions of the north shore of Lake Superior made collections of plants on Isle St. Ignace in 1866, and on Michipicoten Island in 1869. Some specimens from the latter location are in the herbarium of the University of Michigan (MICH), including the only known (and as yet unconfirmed) report for *Dryas drummondii* from that part of Lake Superior.

In 1869, John Macoun (1831-1920), the first naturalist appointed to the Geological Survey of Canada, spent nearly two months collecting plants on the shores of Lake Superior and comparing his observations with those reported by Agassiz. He noted particularly that tundra-like habitats and arctic-alpine species of plants were found only in areas along or close to the shore of the lake and that, as soon as he moved away from the cooling influence of the lake, the vegetation reverted to a mixed forest not very different from the type he knew just north of Belleville on Lake Ontario. Again in the early summer of 1872 Macoun collected at numerous localities from Sault Ste. Marie to Thunder Bay (then known as Prince Arthur's Landing). On a third visit in 1884, Macoun obtained specimens from Michipicoten, Gull Island, Red Rock, Nipigon River and the eastern shores and islands of Lake Nipigon. Macoun's name is commemorated in Macoun Island which is between Nipigon and the Sibley Peninsula on the north shore of Lake Superior (our site no. 46, Appendix B).

In 1891, L.S. Cheney (1858-1938), an American botanist and later a professor at the University of Wisconsin, explored the flora of northern Wisconsin, part of the north shore of Lake Superior and the region along the Minnesota-Ontario boundary. At Grand Portage he found *Vaccinium uliginosum* and *Castilleja septentrionalis*, both of which are rare on the western portion of the Lake Superior shore.

After the turn of the century, botanical activity in the Lake Superior region increased as new roads began to link up communities along the shore. It was not until 1960, however, that the last link in the Trans-Canada Highway between Wawa and Marathon was completed. From the numerous names of botanists and others who have collected plants around Lake Superior since 1900 we mention only a few.

Professor F.K. Butters of the University of Minnesota began collecting in Cook County, Minnesota in 1924 and was assisted by several colleagues, notably later, in 1936 and 1937, by E.C. Abbe. Attention was soon focussed on the rare plants of the Lake Superior shore, the islands nearby, and the lakes and adjacent cliffs (Border Lakes) along the boundary between Minnesota and Ontario. The results of this long-term study again called attention to arctic-alpine as well as to other rare plants in the Lake Superior region (Butters & Abbe, 1953).

The University of Toronto and the National Museum of Canada jointly sponsored botanical surveys in five main areas between Sault Ste. Marie and Thunder Bay in the summers of 1935 through to 1939. Large series of specimens were collected by T.M.C. Taylor, R.C. Hosie, S.T.B. Losee, M.W. Bannan, H.M. Harrison and others (in various combinations). The areas visited were: Batchawana Bay, 1935: Sibley Peninsula, 1936; Schreiber and the Slate Islands, 1937; Michipicoten, 1938; and Peninsula (now Marathon), 1939. The only report published on this project was that for the first year at Batchawana (Hosie, 1938). The first two sets of specimens are in the National Herbarium of Canada (CAN) and the University of Toronto (TRT), but duplicates were widely distributed to other herbaria in Canada and abroad.

Our knowledge of the flora of the Thunder Bay District owes a great deal to the energetic field work carried out over a period of about forty years by C.E. Garton of Thunder Bay. He began collecting on the mainland but soon included visits to the off-shore islands in Lake Superior, where he found *Saxifraga tricuspidata*, previously known in the area only from Isle Royale, Michigan, and adjacent islands near its northeast end. Garton also discovered *Pyrola grandiflora* in Ouimet Canyon in 1969 and *Arenaria humifusa* in a canyon at Cavern Lake in 1972. Complete or partial sets of Garton's collections, which, including duplicates probably exceed 40,000, are filed at CAN, DAO, LKHD, MICH and TRT.

As part of a programme of botanical exploration in Ontario which he started while on the staff of the Department of Botany, University of Toronto, J.H. Soper collected at various locations along the Lake Superior shore from 1960 to 1973. On a trip in 1961 with P.F. Maycock, an examination was made of vegetation on the cliffs and rocky ledges along the shore of Old Woman Bay, south of Wawa, resulting in the description of a well-defined community of arctic-alpine plants, the first for the east shore of Lake Superior. (Soper & Maycock, 1963). In 1964, J.H. Soper and F.A. Fraser rediscovered *Cypripedium passerinum* at the mouth of the Pic River, confirming the persistence of the species in this disjunct location where it had first been collected ninety-five years earlier by John Macoun. Collections by Soper are mainly at CAN and TRT.

E.G. Voss, University of Michigan, has made six collecting trips and has led twelve student field trips to a number of sites on the north shore of Lake Superior; also four major botanical expeditions to Isle Royale, Michigan (including neighbouring islands at the northeast end). The first set of specimens resulting from these trips is in the herbarium at Ann Arbor (MICH).

J.K. Morton, University of Waterloo, has recently made several trips to the Lake Superior region, collecting at several sites where arctic-alpine species are known, for example the Border Lakes, Sibley Peninsula and the Slate Islands. He has also visited Caribou Island, near the international boundary in the eastern part of the lake. Morton's collections are at the herbarium of the University of Waterloo (WAT).

In the preceeding section, the abbreviations for herbaria are the internationally recognized codes published in Index Herbariorum and its Supplements (Holmgren & Keuken, 1974).

Scope of the present study. — David R. Given worked at the National Herbarium, National Museum of Natural Sciences, Ottawa, as a National Research Council post-doctoral fellow from 1973 to 1974. He carried out literature, herbarium and field studies aimed at an analysis of the arctic-alpine element in the flora of the Lake Superior

Fig. 2. Spar Islet, Leadman Islands (Typical of islets along the Lake Superior shore; arctic-alpine plants occur on the rock faces.)

region. Field work in 1973 by Given and Soper was concentrated on areas considered to be imperfectly studied, e.g., Pic Island, Black Bay Peninsula and the islets between Sibley Peninsula and Nipigon, but included a wide range of representative sites and certain localities known to be of particular floristic interest and richness, such as the Slate and Leadman Islands, and a canyon at Cavern Lake (Fig. 2).

Later in the summer of 1973, field work was carried out by Given and Soper in the Selkirk Mountains of British Columbia and Given also spent two weeks in the mountains of Colorado. These alpine studies enabled comparisons to be made with regions characterized by alpine or arctic-alpine disjunct floras. The extensive literature and herbarium searches by Given yielded numerous floristic records which were important in assessing the known ranges of arctic-alpine species.

THE ARCTIC-ALPINE FLORISTIC ELEMENT

Wulff (1943) defined the arctic-alpine floristic element as that group of species having areas with one part lying in alpine regions and the other in the Arctic, the latter generally being defined as the treeless tundra of the far north with the tree-line, or poleward limit or arborescent conifers, forming a boundary between the arctic and subarctic zones (Young, 1971). Figure 3 shows the distribu-

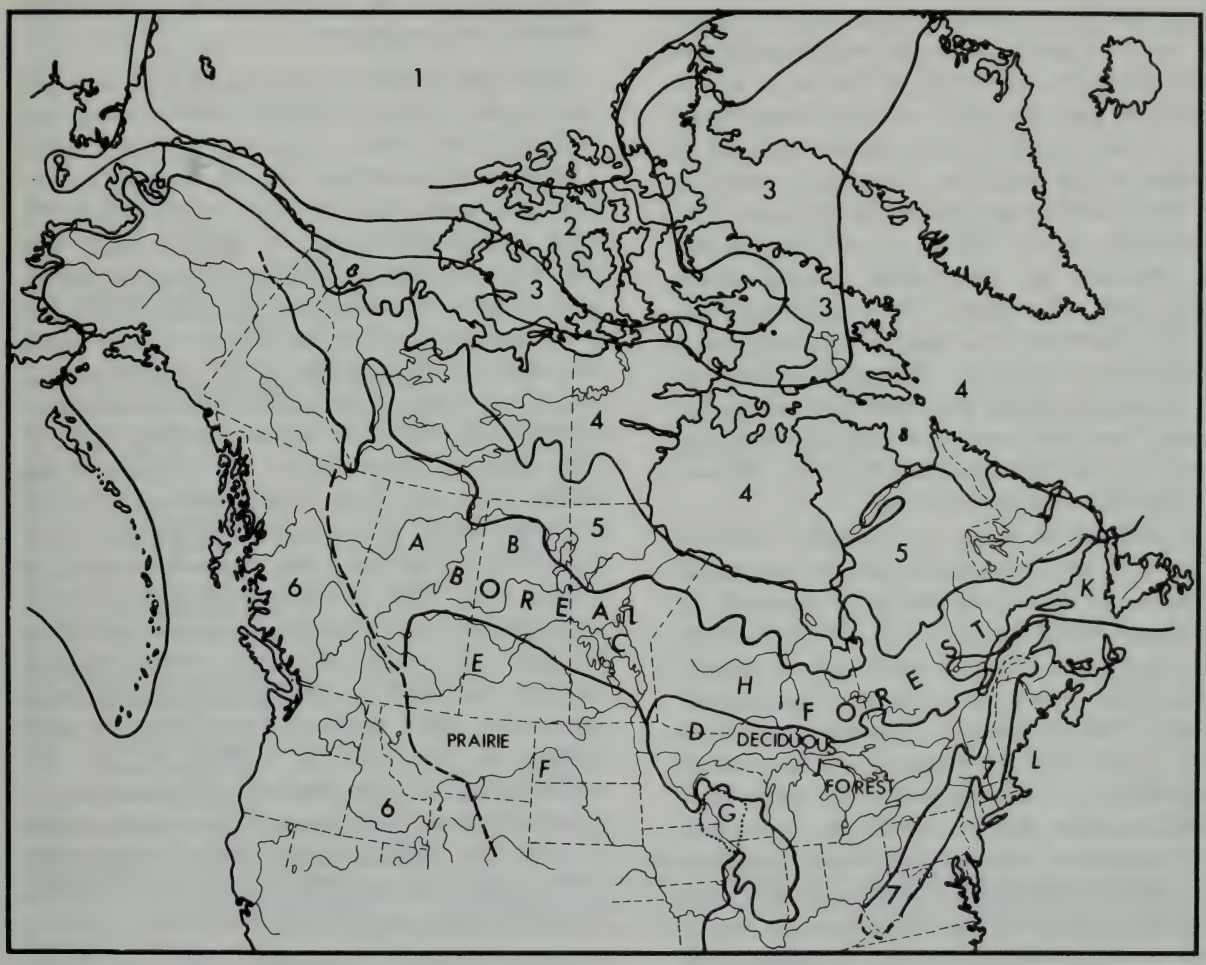

Fig. 3. Generalized vegetation zonation. 1, extreme-arctic; 2, high-arctic; 3, mid-arctic; 4, low-arctic; 5, subarctic; 6, western mountains (cordillera); 7, eastern mountains.

tion of vegetation zones discussed in this paper. The zone boundaries do not always follow those of Young as they have been modified to accomodate the zone boundaries proposed by Porsild (1958) and by a consideration of the species ranges illustrated by Porsild (1964).

In a strict sense, Wulff's definition does not include areas such as Lake Superior which are neither alpine nor arctic. It is convenient, however, to retain the term for species having their main areas in alpine or arctic regions but which also occur in scattered localities elsewhere as components of open communities lacking trees and tall shrubs. Quaternary studies often suggest that such occurrences, disjunct from the chief areas of distribution, are relics of wider, earlier distributions or that the plants involved have migrated and persisted following glacial retreat.

Geological evidence strongly supports the view that the Lake Superior basin was ice-filled during the Wisconsin glaciation with complete extinction of flora and fauna. As ice sheets receded, many sites were occupied by species which today are found typically in the Arctic. Migration of arctic-alpine taxa into the area probably commenced about 11,000 years B.P. as ice melted back out of the basin for the last time. It probably ceased as the climate ameliorated about 10,000 years B.P. and allowed spruce forest to colonize ice-free areas without an intervening tundra phase (Ogden, 1967; Terasmae, 1967). Although this period of migration was reasonably synchronous with the retreat of the ice, Terasmae pointed out that several late-glacial migration routes into the area may have been used; these could be regarded as separate migration elements but their delineation is fraught with uncertainties.

It is difficult to make a rigorously objective definition of the arctic-alpine element and to set up criteria for the identification of members of this element which would satisfy everyone. Most authors have agreed upon a small core of species, including such widespread plants as *Saxifraga aizoon* and *Trisetum spicatum*. Some accounts have included taxa better regarded as boreal (*Ledum groenlandicum*, *Picea mariana*) while others have omitted low-arctic species such as *Sagina nodosa*. In some instances, taxonomically doubtful entities have been included and a few records have been perpetuated even though based on erroneous reports or misidentifications. We have selected 48 species which we regard as constituting the arctic-alpine element of the Lake Superior flora (Table 1) and will discuss below the criteria used in making this selection.

In circumscribing the arctic-alpine element at Lake Superior, primary consideration has been given to contemporary distribution patterns. Curtis (1959) defined floristic elements as containing taxa each of which shares a common type of current geographical range. This echoes the earlier usage by Braun-Blanquet (1923) who considered an element as the floristic and phytosociologic expression of a territory of limited extent, including thereby the taxonomic units and the phytogeographic groups characteristic of a given region. In contrast, Wulff (1943) argued for a wider use of the term to include genetical, migrational, historical and ecological as well as geographical elements. Wulff considered that all these aspects must he taken into consideration before conclusions are reached on the history and development of a flora but be conceded that geographical elements are fundamental.

Several arctic-alpine species have been reported from Lake Superior without substantiating herbarium specimens. Agassiz (1850) listed *Loiseleuria procumbens* but no specimens have been seen and it has not been recollected in the area. *Ledum decumbens* was mapped by Hultén (1970) as occurring at Lake Superior and at several sites in southern Manitoba. Scoggan (1957) has suggested that the latter are almost certainly based on misidentified specimens of *L. groenlandicum*, which is frequent in the boreal forest as an understorey shrub. The same explanation may apply at Lake Superior; no specimens of *L. decumbens* are known from the shore of the lake nor from its drainage basin. Other unverified records from Lake Superior include *Carex heleonastes* (cited by Dutilly *et al*, 1954, on the basis of a record from Thunder Bay) and *Cassiope hypnoides* (noted by Upham, 1883, from Minnesota Point). Several records were based on definite misidentifications and a few were rendered superfluous through changes in the usage of epithets or the circumscription of taxa. Records, for example, of *Euphrasia* from Lake Superior are suspect, since Sell and Yeo (1970) indicated in their revision that considerable confusion has existed in the application of names to individual specimens.

Criteria adopted. — Our criteria have almost certainly eliminated from our final list several species

Table 1. The Arctic-alpine floristic element of the Lake Superior basin — Distribution outside the region

Life Form	Species	Distribution N. American Arctic: Extreme Arctic	High Arctic	Mid-Arctic	Low Arctic	Subarctic	Distribution in North America south of the Arctic: Alpine: Cordillera	Eastern Mts.	Boreal Alberta	Boreal Saskatchewan	Boreal Manitoba	Minnesota-Ontario	Canadian Prairies	American Prairies	Driftless Area	Boreal Ontario	Great Lakes (Other)	Gulf of St. Lawrence	Eastern Coastline
		1	2	3	4	5	6	7	A	B	C	D	E	F	G	H	J	K	L
Hs	Festuca brachyphylla	o	o	o	o	+	+	+	.	.	.	.	+	+	.	.	.	+	.
Hs	Saxifraga cernua	o	o	o	o	+	+	+	+	.	.	.	.	+	.	.	.	.	.
Ch	Dryas integrifolia	+	o	o	o	o	+	+	.	.	.	.	.	.	.	.	.	+	.
Gst	Polygonum viviparum	+	o	o	o	o	+	+	.	.	.	.	.	.	.	.	.	+	.
Ch	Cerastium alpinum	.	o	+	+	.	+	.	+	.	.	.	.	.	.	.	.	+	.
Hs	Senecio congestus	.	o	o	+	+	.	.	+	.	+	+	.	.	+	.	+	.	.
Hs	Trisetum spicatum	.	o	o	o	+	+	+	.	.	+	.	.	.	.	.	+	+	.
Ch	Saxifraga tricuspidata	.	o	o	o	o	+	.	+	+	+	.	.	.	.	.	.	.	.
Hrr	Pyrola grandiflora	+	+	o	o	+	+	.	+	.	.	.	.	.	.	.	.	+	.
Hr	Woodsia glabella	+	+	o	o	+	+	+	.	+	+	.	.	.	.	.	.	+	.
Ch	Astragalus alpinus	.	+	o	o	o	+	+	+	+	+	.	.	+	.	.	+	+	+
Ch	Empetrum nigrum	.	+	o	o	o	+	+	+	+	+	.	+	.	.	.	+	+	+
Ch	Lycopodium selago	.	+	o	o	o	+	+	.	.	+	+	.	.	+	+	+	+	+
Hs	Poa glauca	.	+	o	o	o	+	+	+	+	+	.	+	.	.	+	+	+	+
Hr	Dryopteris fragrans	.	.	o	o	+	+	+	.	.	.	+	.	.	+	.	+	+	+
Grh	Elymus mollis	.	.	o	o	+	+	.	.	.	.	+	.	.	.	.	+	+	+
Ch	Vaccinium uliginosum	.	.	o	o	+	+	+	.	.	+	+	.	.	.	+	.	+	.
Hs	Carex capillaris	.	.	o	o	o	+	+	+	+	+	+	+	.	.	+	+	+	+
Grh	Carex scirpoidea	.	.	o	o	o	+	+	+	+	+	+	+	.	.	.	+	+	.
Ch	Arenaria humifusa	.	+	+	o	+	+	+	.	.	.	.	.	.	.	.	.	+	.
Hr	Woodsia alpina	.	+	+	o	+	.	.	.	.	.	.	.	.	.	.	.	+	.
Grh	Carex saxatilis	.	.	+	o	+	+	.	.	+	+	.	.	.	.	.	.	+	+
Grh	Carex supina	.	.	+	o	+	.	.	+	.	+	+	+	.	.	.	.	.	+
Ch	Draba norvegica	.	.	+	o	+	.	.	.	.	.	.	.	.	.	.	.	+	.
Ch	Saxifraga aizoon	.	.	+	o	+	.	+	.	.	+	.	.	.	.	.	+	+	+
Hsr	Anemone parviflora	.	.	+	o	o	+	+	+	.	.	.	.	.	.	.	+	+	.
Hsr	Calamagrostis stricta	.	.	+	o	o	+	+	+	+	+	.	+	+	.	.	+	+	+
Hsr	Calamagrostis purpurascens	.	.	+	o	o	+	.	+	.	.	.	+	.	.	.	.	+	.
Ch	Vaccinium vitis-idaea	.	.	+	o	o	+	+	+	+	+	+	.	.	.	.	.	+	+
Hp	Castilleja septentrionalis	.	.	.	o	+	.	+	.	.	.	.	.	.	.	.	.	+	.
Hs	Draba incana	.	.	.	o	+	.	+	.	.	.	.	.	.	.	.	.	+	.
Ch	Draba aurea	.	.	.	o	o	+	.	+	+	.	.	+	+	+	.	.	+	.
Hr	Pinguicula vulgaris	.	.	.	o	o	+	+	+	+	.	+	.	.	.	+	+	+	.
Hs	Poa alpina	.	.	.	o	o	+	+	.	.	+	.	.	+	.	.	+	+	.
Hrr	Ranunculus lapponicus	.	.	.	o	o	+	+	+	+	+	+	.	.	.	+	.	+	.
Hr	Scirpus cespitosus	.	.	.	o	o	+	+	.	+	+	.	.	.	.	.	+	+	.
Hr	Tofieldia pusilla	.	.	.	o	o	+	.	.	.	+	.	.	.	.	.	.	+	.
T	Euphrasia hudsoniana	.	.	.	+	o	.	.	.	.	+	.	.	.	.	.	.	.	.
Hp	Hedysarum alpinum	.	.	.	+	o	.	+	.	.	.	+	+	.	.	.	.	+	.
Ch	Lycopodium alpinum	.	.	.	+	o	+	.	.	.	.	.	+	.	.	.	.	+	.
Hsr	Phleum alpinum	.	.	.	+	o	+	+	.	.	.	.	+	+	+	.	.	+	.
Hs	Sagina nodosa	.	.	.	+	o	.	+	.	.	+	.	.	.	.	.	.	+	+
Ch	Selaginella selaginoides	.	.	.	+	o	+	+	.	.	.	.	.	.	.	.	+	+	+
Hsr	Tanacetum huronense	.	.	.	+	o	.	+	.	.	.	.	.	.	.	.	+	+	.
Hr	Taraxacum ceratophorum	.	.	.	+	o	+	.	+	+	.	.	.	.	.	.	.	+	.
Ch	Potentilla multifida	.	.	.	.	o	.	.	.	.	+	.	.	.	.	.	.	.	.
Hr	Primula mistassinca	.	.	.	.	o	.	.	.	.	+	.	.	.	+	+	+	+	+
N	Salix myrtillifolia	.	.	.	.	o	+	.	+	+	+	.	+	.	.	+	.	+	+

KEY: o – common or widespread in zone (applies to zones 1–5 only); + – present in region or zone.
LIFE FORM SYMBOLS: Ch – chamaephyte; Grh – rhizome geophyte; Gst – Stem-tuber geophyte; Hp – protohemicryptophyte, without runners; Hr – hemicryptophyte, rosette, without runners; Hrr – hemicryptophyte, rosette, with runners; Hs – hemicryptophyte, semi-rosette, without runners; Hsr – hemicryptophyte, semi-rosette, with runners; N – nanophanerophyte, 25 cm to 2 m in height; T – therophyte, plant annual (for complete classification see Scoggan, 1978, Table 3, p. 21.)

which, on further investigation, will merit inclusion. However, this ensures that the present list of arctic-alpine taxa includes only those for which we have adequate data and can be reasonably certain of their occurrence in the area.

(a) Geographical distribution

Taxa must be verified as occurring within the Lake Superior watershed and elsewhere be almost exclusively confined to arctic or alpine habitats (Fig. 4). This excludes many widespread arctic species such as *Equisetum arvense*, which is both arctic and also common in boreal and temperate regions. Also excluded are *Campanula rotundifolia*, *Hippuris vulgaris* and *Pyrola minor*, which extend into a diversity of habitats well south of the Arctic.

A small number of species typical of areas in the Low Arctic and Subarctic of the Canadian mainland generally fail to reach the higher arctic regions on the islands to the north (Table 1). Such marginally arctic taxa were considered individually, their inclusion dependent not only on an overall geographical range but on local patterns of distribution and association with other arctic-alpine species. A few species such as *Primula mistassinica* are included because, although they do not occur north of the Low Arctic, they are intimately associated with typically arctic-alpine species throughout much of their range and even in boreal zones are almost exclusively on lakeshores or rock outcrops.

Some species, including *Lycopodium selago* and *Calamagrostis stricta*, are found at numerous sites; others, such as *Dryas integrifolia* and *Arenaria humifusa*, occur at very few. Species which at southern sites are restricted to enclaves of open vegetation, including rock outcrops, lakeshores, stream sides, cliffs and bogs, may be regarded generally as legitimate members of the arctic-alpine element. At these sites, local microclimate, topography and soils act in concert to maintain habitats simulating those of arctic and alpine regions. In contrast, taxa are not included when they form an integral part of typically boreal or temperate communities.

The distribution of members of the arctic-alpine element at Lake Superior is essentially disjunct, being separated from main distribution areas in alpine regions and in the Arctic by an extensive zone of boreal coniferous forest. Only where favourable local deviations of habitat allow, do enclaves persist and connect Lake Superior stations with those far to the north.

(b) Ecological association

A marked feature of most of the arctic-alpine taxa acceptable for the Lake Superior area is their occurrence in many and varied combinations to form discrete communities contrasting sharply with surrounding boreal (chiefly coniferous) forest vegetation. First consideration has been given to those species so found, although in a few instances (for example, *Lycopodium selago*, *Dryopteris fragrans* and *Saxifraga aizoon*) isolated stations of single species not associated with other arctic-alpine plants are known. Numerous taxa were rejected because, although they occur with plants found in the Arctic, their ecological amplitude commonly allows them to infiltrate boreal and temperate communities.

(c) Taxonomic status

In some instances we have been unable to decide whether a taxon occurring at Lake Superior is identical with the one occurring in the Arctic. In other cases the taxon belongs to a complex in which the taxonomic boundaries are not clearly defined. As an example, the distribution of *Carex norvegica* was mapped by Porsild (1964) as a low-arctic species ranging south to James Bay in eastern Canada. It is recorded from Lake Superior but not from the intervening Hudson Bay Lowlands. However, Hitchcock *et al.* (1969) and Boivin (1967) placed it in synonymy with the more widely distributed *C. media* and, according to Hitchcock *et al.*, *C. norvegica* includes specimens sometimes referred to *C. halleri sensu lato*. Accurate maps cannot be constructed without seeing all relevant herbarium material or knowing in what sense each collector named his specimens. Similar difficulties led to the rejection of species of *Artemisia*, and in particular *A. borealis*, which Polunin (1940, p. 362) appropriately called a "bad typus polymorphus."

Thus, a conservative approach has been adopted. For example, all forms of *Empetrum* in the Lake Superior region have been treated under the single species *E. nigrum* although various specific epithets have been applied to material from that region. Butters and Abbe (1953) distinguished two taxa in northeastern Minnesota

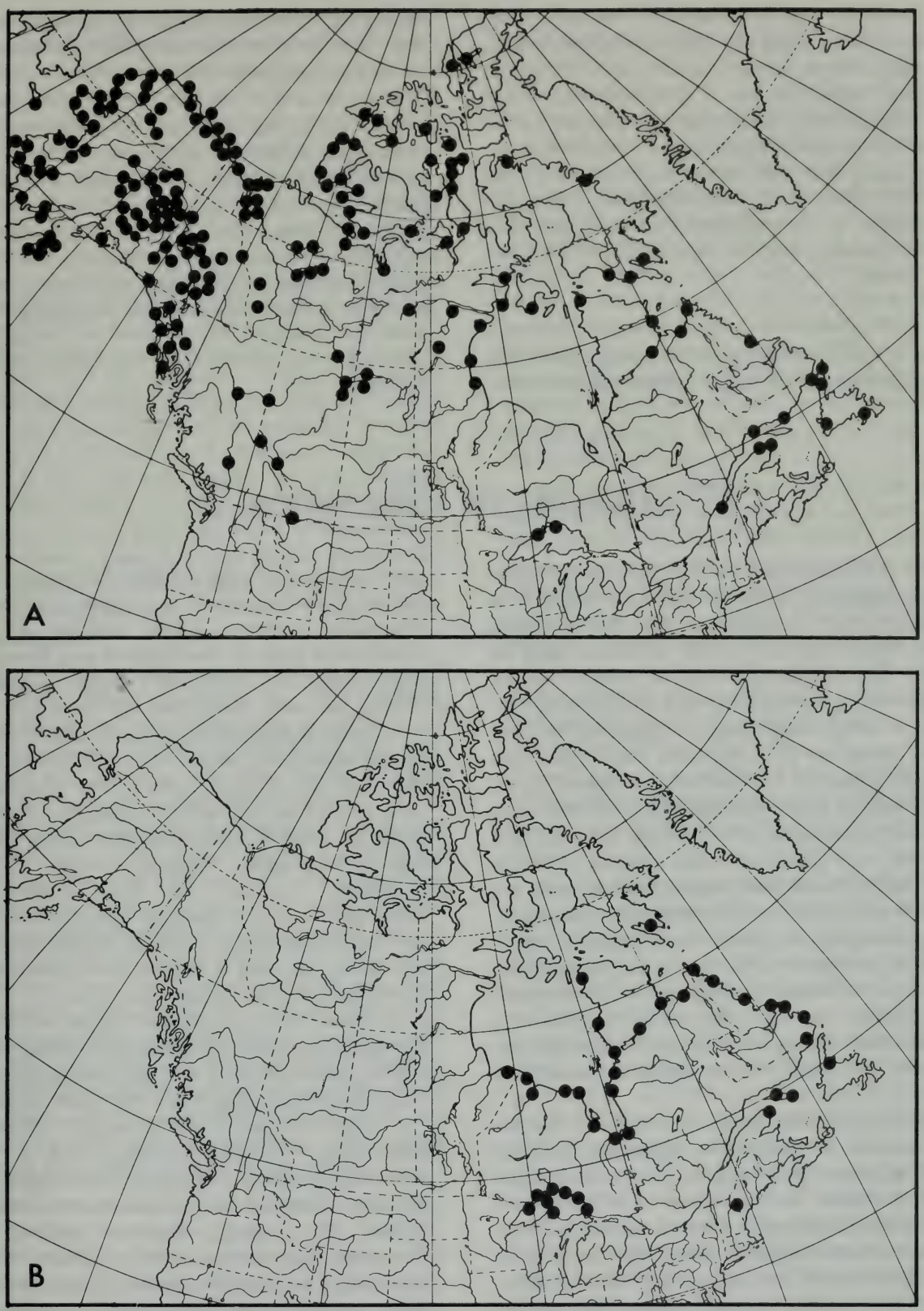

Fig. 4. North American examples of arctic-alpine distributions: A, *Cerastium alpinum* (*sensu lato*); B, *Castilleja septentrionalis*.

near the lake and commented on the differences between them, using the names *E. nigrum* and *E. atropurpureum*. Other names used for Lake Superior specimens are *E. hermaphroditum* and *E. eamesii*; these taxa being distinguished on the basis of various combinations of morphological, cytological and distribution evidence. However, Hultén (1970, p. 86) concluded that *Empetrum* constitutes a "complicated complex where different authors rarely, if ever, arrive at the same conclusion."

(d) Lack of data

In a few instances, apparent geographical disjunctions may have resulted from lack of collecting in the intervening areas. For example, mapping the Ontario records for *Cypripedium passerinum* suggests that this species is disjunct with areas in the Low Arctic and Subarctic and along the northern shore of Lake Superior. It has not been collected from the boreal forest separating these areas. Farther west in Canada, however, it occurs in moist coniferous woods well within boreal coniferous forest boundaries, associated with various species, including *Shepherdia canadensis*, *Picea glauca* and species of *Salix*. It is possible that the Lake Superior stations will eventually be connected to those around James Bay by colonies in the intervening forested lowlands.

SAMPLING OF VEGETATION

Hosie (1938) provided the first published account of the vegetation of the shore of Lake Superior at a specific site, Batchawana Bay. He discussed talus, sand beaches and the xerosere, each of which may include arctic-alpine species. Arctic-alpine vegetation was dealt with mainly in descriptions of the xerosere along the rugged rocky shore from Mamainse Point to Mica Bay. Comments were informal but he observed that habitat conditions must be severe with plants largely dependent for moisture on dew, direct rainfall and mists and with the rock substrate wholly exposed to sweeping winds. At such sites, smooth rock surfaces are matted with lichens and xerophytic mosses assist the spreading of plants that occupy nearby crevices in which materials can accumulate and retain some moisture. He regarded the crevices and pools as of particular importance in providing places where shrubs and trees could grow, leading in time to heath or low-canopied coniferous forest.

Butters and Abbe (1953) produced informative descriptions of tundra-like vegetation in Cook County, Minnesota, along the northwest shore of Lake Superior. They were particularly interested in disjunct occurrences of arctic-alpine and cordilleran plants although they did not clearly distinguish which species were regarded as arctic or boreal in affinity. Among the species listed for "cold, wet rocks and ledges along the Lake Superior shore" (ibid, p. 51) are *Selaginella selaginoides*, *Tofieldia pusilla*, *Polygonum viviparum*, *Epetrum nigrum*, *Vaccinium uliginosum*, *Pinguicula vulgaris*, *Sagina nodosa*, *Primula mistassinica* (incl. *P. intercedens*) and *Euphrasia hudsoniana*. The habitat is evidently similar to Hosie's xerosere with areas of bare rock and crevices but greater attention was drawn to spring-fed or seepage-fed pools which were described as abundant. At the upper limit of this shore zone, some of the plants occurred in sphagnous cushions about the bases of scattered shrubs such as *Potentilla*, *Physocarpus*, *Kalmia*, *Ledum*, *Chamaedaphne*, *Vaccinium* and *Salix*. Butters and Abbe (1953, p. 52) described moist shady cliffs and cool canyon walls inland from Lake Superior as "most productive in the search of these localized habitats in Cook County for rarities . . . ." As in the case of shoreline habitats, here also arctic-alpine plants often have an almost random occurrence. Some occur only at single sites, an example being *Saxifraga cernua* which was found covering ". . . but a few square feet at the top of a single talus slope." (Butters & Abbe, 1953, p. 52). Arctic-alpine plants noted from these inland cool sites are *Calamagrostis purpurascens*, *Woodsia alpina*, *W. glabella*, *Saxifraga aizoon* and *Cerastium beeringianum* (= *C. alpinum*). A further category of habitat mentioned by Butters and Abbe includes south-facing cliffs and cliff-tops lithologically similar to the cooler sites but exposed to the sun and consequently warmer and drier.

Most of the plants at such sites are temperate continental species but occurring with them are more northern taxa such as *Vaccinium uliginosum* and *Draba norvegica*.

Descriptions of the shoreline tundra strip are found in a series of papers on boreal hepaticae of Minnesota and adjacent regions (Schuster 1957, 1958a, 1958b). Although Schuster commented that this area was rich in arctic-alpine elements, he added that none of the hepaticae of the zone could be regarded as strictly arctic but were arctic-alpine or "low-grade arctic types" (Schuster, 1958b, p. 268).

Of forty-four hepaticae showing an arctic-alpine distribution in Europe and North America, Schuster recognized twenty as occurring along the shore of Lake Superior. As Butters and Abbe had found with vascular plants, so too Schuster reported (1958a, pp. 270-1) that hepaticae are in many instances extremely local in distribution, often being known from only one or two colonies, for example *Anastrophyllum saxicolus* at Pigeon Point and *Lophozia quadriloba* on Keweenaw Peninsula.

At Old Woman Bay, south of Wawa, Soper and Maycock (1963) provided the first detailed analysis of the tundra-like shore vegetation at a specific locality. Within the bay *Polygonum viviparum* and *Sagina nodosa* grow among boulders and pebbles at the upper end of the beach next to boreal forest. Exposed rock ledges encrusted with lichens and mosses provide niches for *Saxifraga aizoon*, *Primula mistassinica* and *Pinguicula vulgaris*; at the edges of temporary rock pools and seepages are tussocks of *Scirpus cespitosus* and *Carex scirpoidea*. Overlooking these sites, along the shore, and the steep sides of chasms, they found *Woodsia alpina*, *W. glabella*, *Dryopteris fragrans* and *Lycopodium selago*. It was recognized that these habitats are represented elsewhere around Lake Superior and subsequent field work at Pointe aux Mines revealed that there, too, extensive communities containing arctic-alpine plants were well-developed (Soper 1963).

General practice has been to avoid categorizing arctic-alpine vegetation types at Lake Superior. Hosie (1938) referred to a xerosere and several authors have given lists of plants, including arctic-alpine species, occurring on rocky shores, rock ledges and in crevices (e.g., Fernald, 1935; Butters & Abbe, 1953; Wells & Thompson, 1974). Soper and Maycock (1963) described a community as arctic-alpine and Schuster (1957, 1958a, 1958b) referred to a tundra strip and a tundra biome. Although sometimes in the past the term tundra has had quite a precise meaning, it now tends to be used so loosely as to be relatively meaningless. Even within the expanded use of the term, it is doubtful whether the term tundra can be used properly to refer to the open shoreline communities at Lake Superior. Few of the physical attributes of arctic or alpine tundra such as low summer temperatures and presence of a partial or a permanent permafrost actually characterize the shoreline sites. Shore vegetation might be called tundra or tundra-like in appearance, but that of canyons can scarcely be regarded as such, yet the latter is not necessarily sharply demarcated in the field from more open habitats.

In some very exposed shoreline habitats arctic-alpine plants may be dominant but more often they are co-dominant with shrubby and herbaceous boreal species. At one extreme, cliff or talus-slope communities with only one or two arctic-alpine species may be regarded as arctic-alpine vegetation merely because these few species are present. In fact, they may, with greater justification, be considered prairie or boreal communities because of the preponderance of species with prairie or boreal affinities. We use "arctic-alpine" for all vegetation at Lake Superior containing arctic-alpine species; the reader should, however, be aware of our broad interpretation of the term.

The community types that are described in this paper are broad mapping units based on vegetation appearance and floristic composition; the community type is delimited here as a group of stands of similar plant composition associated with one particular type of site, e.g. canyon floors or shore platforms. The community concept used in this study should not be construed as indicating necessarily any inherent interrelationships between members of a community. Many of the stands sampled are extremely open with individual plants separated by areas of bare rock. In such instances plants exert little or no influence on each other and each particular site might be best regarded as a mosaic of micro-associations which collectively make up a heterogeneous but recognizable unit of vegetation. We have not generally studied the micro-associations of the individual crevices, ledges or pools in detail.

Descriptive names of communities are a combination of conspicuous though not necessarily dominant plant species, overall vegetation type (e.g., herbfield, heath, shrubland, etc.) and topography. This allows quick recognition of a particular vegetation unit in the field without the necessity of detailed quantitative analysis.

Analysis of sampling. — Sophisticated vegetation sampling was not undertaken for two reasons. Firstly, the general nature of arctic-alpine communities, with large bare areas of rock and scattered individual plants often confined to crevices, does not lend itself to methods better suited to more closed communities. Frequently, only one plant of a particular species might be encountered in a stand and rarely were there more than twenty or thirty individuals. For each stand (see Appendix B for details of their location) a list was made of all species of vascular plants present with notes on vegetation structure and site characteristics. Where warranted, abundance was noted on a combined value abundance scale, dominance and sociability each being scored on a 5 to + scale (see Table 4 for explanation). Secondly, simple analytical methods allowed us to cover a wide range of sites in a relatively short time and a principal aim was to sample a wide range of community types rather than to concentrate on only a few sites.

Stands were arranged by the use of sociological tables into groups and subgroups representing classes and communities. Confirmation of these was by means of numerical analyses carried out by Dr. D.A. Ratkowsky of the CSIRO Regional Laboratory, Hobart, Australia. Use was made of a wide variety of clustering algorithms but well-defined groups proved difficult to distinguish. The most consistent results came from three programmes: Maximal Predictive Classification (Gower, 1974), which is available as an option in the CLASSIFY directive of GENSTAT, DIVINF (Lance & Williams, 1968) and REMUL (Lance & Williams, 1975). Of these, the last accepted multistate characters but, for the other two, species distributions had to be expressed as presence and absence only.

The most meaningful results were obtained when all the rarely-occurring species were eliminated and the analyses were confined to the fifty species present in at least four stands. Criteria for an optimum number of groups in the REMUL analyses showed that this was probably either three or four. The 2-, 3- and 4-class solutions were asked for with REMUL, Maximal Predictive Classification (MPC) and DIVINF. Aggregates of stands preserved throughout analyses were:

Aggregate A	consisting of relevés 7,44,3,4.
B	31,28,21,33,6,27,1, 5,35,11,36,45,41.
C	9,46,26,24,18.
D	8,14,13,15,47,17.
E	23,22,29,19,20,10.
F	16,42,25,43.
G	34,37,30.
H	2,38,40,39.
I	12,32.

The disposition of these aggregates is shown in Table 2. Two primary classes were formed, one of aggregates A,G,C,D, and I; the other being formed by the remainder.

To test the integrity of such classing and of the aggregates, a nearest neighbour similarity matrix was computed (Table 3). This utilized all species records in the stand but reduced them to presence and absence. Joint absences (i.e., where both stands lacked a species) were discarded and using the remainder a percentage similarity coefficient (actually the classic Jaccard coefficient) was calculated for each stand and its five nearest neighbours (i.e., those other stands which were most similar in species composition):

$$\% \text{ Similarity} = \frac{\text{No. of } +/+ \text{ combinations} \times 100}{\text{No. of } +/+ \ + \text{ No. of } \mp/- \text{ combinations}}$$

Table 3 shows why stands 7,44,3,4, form a tightly-knit group (assemblage A) which is consistently preserved regardless of the algorithm used. None has particularly high percentage similarities (ranging from 31.0% to 40.7%) but each member of this group is closer to each other member than it is to any other stand.

Comparison of the nearest neighbour table (Table 3) with groupings suggested in the class with A,G,C,D, 12 and 32 confirms that these are reasonably closely linked entities probably representing real aggregates. However, the table does not do this for the remainder, indicating instead that many stands have little in common

besides being generally dissimilar to everything else. Examination of the site details shows that they come from a great diversity of locations. Stands from distinct habitat types were extracted and treated as distinct groups:

(a) Cliff sites: stands 33,20,25,27 and 11
(b) Talus slope sites: stands 28 and 22
(c) Mat plant dominated sites: stands 5 and 45
(d) Intermediate forest-shoreline sites: stands 23 and 16.

Of the remainder, stand 36 is from a site with only four species and was sampled to represent the most exposed and wave-washed site near water level.

Table 2. 4-, 3-, and 2-Group Solutions using the Computer Strategies REMUL, MPC and DIVINF.
Letters refer to aggregates on page 12.

Strategy	4-group solution	3-group solution	2-group solution
REMUL	A	A	A + C + D + G + I
	G		
	C + D + I	C + D + G + I	B + E + F + H
	B + E + F + H	B + E + F + H	
MPC	A + G + I	A + G + I	A + G + I + (9,18,46 of C) + (31 of B) + (47 of D)
	C + D	C + D	
	B + (39,40 of H)	B + E + F + H	E + F + I + (24,26 of C) + (remainder of B) + (remainder of D)
	E + F + (2,38 of H)		
DIVINF	A + C + (34,37 of G) + (2 of H)	A + C + (34,37 of G) + (2 of H)	A + C + D + E + G + H + I
	D + E + I + (30 of G)	D + E + I + (30 of G) + (38,39,40 of H)	
	(38,39,40 of H)		B + F
	B + F	B + F	

Table 3. Similarity Matrix Neighbours Table
(In each nearest neighbour column the first figure is the stand number, the second is % similarity)

Stand	Nearest Neighbour columns									
	First		Second		Third		Fourth		Fifth	
1	14	25.0	37	25.0	17	21.4	13	21.1	36	20.0
2	42	28.6	46	28.1	34	27.6	10	23.8	44	23.3
3	44	40.7	4	37.5	34	35.7	7	31.0	37	30.8
4	3	37.5	44	37.0	7	32.1	32	31.8	47	29.2
5	16	29.4	45	22.2	7	16.0	26	12.5	32	10.5
6	43	13.3	32	11.1	30	10.5	47	10.0	4	9.5
7	44	40.0	12	32.3	4	32.1	3	31.0	46	24.3
8	9	34.2	13	32.3	26	28.6	47	28.1	14	26.5
9	26	37.5	8	34.2	13	33.3	47	33.3	24	31.3
10	14	35.3	32	27.8	36	27.3	17	26.7	15	25.0
11	27	33.3	25	25.0	41	16.7	33	15.4	20	15.4
12	47	34.6	7	32.3	34	32.3	31	30.0	29	28.0
13	26	36.0	9	33.3	14	33.3	17	33.3	8	32.3
14	17	44.4	10	35.0	13	33.3	15	33.3	47	33.3
15	17	41.2	14	33.3	47	30.4	34	28.6	29	28.6
16	5	29.4	23	25.0	13	20.8	7	20.7	8	17.6
17	14	44.4	15	41.2	47	41.2	13	33.3	19	33.3
18	26	45.5	47	33.3	34	30.8	24	30.4	30	28.6
19	20	57.1	17	33.3	29	27.8	13	23.8	22	23.8
20	19	57.1	17	33.3	29	27.8	22	23.8	14	21.7
21	46	25.8	34	25.0	33	25.0	14	24.0	37	24.0
22	28	29.2	8	24.2	19	23.8	20	23.8	29	22.7
23	28	32.1	16	25.0	13	24.1	22	20.0	3	18.8
24	26	63.6	37	36.0	9	31.3	18	30.4	17	30.0
25	11	25.0	32	20.0	21	19.0	27	18.8	4	17.4
26	24	63.6	18	45.5	9	37.5	13	36.0	47	30.8
27	33	46.2	11	33.3	28	26.3	34	26.1	29	25.0
28	23	32.1	22	29.2	27	26.3	15	24.0	8	20.0
29	34	32.0	17	31.3	13	28.6	26	28.6	47	28.6
30	34	52.2	47	45.0	32	42.1	37	34.8	40	29.4
31	34	33.3	38	33.3	12	30.0	15	21.4	29	19.2
32	47	55.6	30	42.1	34	36.0	46	35.7	4	31.8
33	27	46.2	39	46.2	35	33.3	34	28.0	29	27.8
34	30	52.2	37	46.2	47	44.0	32	36.0	3	35.7
35	39	44.4	33	33.3	41	33.3	29	21.4	21	18.8
36	10	27.3	32	21.4	1	20.0	17	18.2	14	16.7
37	34	46.2	24	36.0	30	34.8	47	33.3	46	31.3
38	31	33.3	40	31.3	39	31.3	12	26.9	34	25.9
39	33	46.2	40	45.5	35	44.4	41	37.5	32	31.3
40	39	45.5	41	37.5	38	31.3	30	29.4	33	26.7
41	40	37.5	39	37.5	35	33.3	33	27.3	42	16.7
42	34	33.3	2	28.6	37	27.3	18	26.3	32	26.3
43	44	19.2	4	18.2	46	16.7	18	15.0	30	14.3
44	3	40.1	7	40.0	46	39.4	4	37.0	34	35.5
45	5	22.2	7	14.3	16	13.3	40	10.0	38	6.7
46	44	39.4	32	35.7	34	35.3	47	33.3	14	31.3
47	32	55.6	30	45.0	34	44.0	17	41.2	12	34.6

Although discrete vegetation units have been described, most are probably part of a continuum. Numerical analyses indicate the fundamental split into rock herbfield and splashpool community classes but also emphasizes that at Lake Superior fine delineation of assemblages of vascular plants is somewhat uncertain and subjective. In delimiting vegetation units, gross characteristics of a site have been given a fundamental place. Finer units have been recognized on the basis of

Table 4. Composition of Shoreline Herbfield Communities

Species	Communities						
	Rock herbfield				Rock-pool herbfield		
	A.1	A.2	A.3	A.4	B.1	B.2	B.3
Achillea millefolium		*	*		*	P	*
Potentilla tridentata		*	*	*	*	P	*
Trisetum spicatum		*	P		*	*	*
Arctostaphylos uva-ursi		P	*	*	*	P	
Campanula rotundifolia	P		*		*	*	P
Potentilla fruticosa		P	*		*	*	P
Solidago randii		P	*		P	P	*
Calamagrostis canadensis		P	P		P	P	*
Alnus crispa			P	P	P	P	P
Arabis lyrata	*		P		*	*	
Sagina nodosa	*		*		P	*	
Empetrum nigrum		P		*		P	*
Primula mistassinica			P		*	*	*
Pinguicula vulgaris			P		P	*	*
Vaccinium uliginosum			P		P	*	*
Scirpus cespitosus			P		*	*	*
Potentilla norvegica	P	P	P			P	
Vaccinium angustifolium		P	P	P			P
Abies balsamea			P		P	P	P
Picea mariana				P	P	P	P
Woodsia ilvensis		*	P		P		
Juniperus horizontalis				*	P	*	
Vaccinium vitis-idaea			P	*			P
Aster ptarmicoides			P		*		P
Polygonum viviparum			P		*	P	
Juniperus communis var. depressa			P		P		*
Deschampsia cespitosa	P	P	P				
Corydalis sempervirens		P	P		P		
Epilobium angustifolium		P	P		P		
Artemisia sp.			P		P	P	
Fragaria vesca			P		P	P	
Poa glauca			P		P	P	
Physocarpus opulifolius			P		P		P
Betula papyrifera				P	P		P
Sorbus decora					P	P	P

* = major contributor to community; P = present in some stands

Other Species (* denotes a major contributor to community)

A.1 *Veronica peregrina* var. *xalapensis.*

A.2 **Festuca brachypylla*, **Saxifraga triscuspidata*, *Deschampia cespitosa*, *Melampryum lineare*, *Saxifraga virginiensis.*

A.3 *Aralia nudicaulis*, *Carex aquatalis*, *C. scirpoidea*, *Cerastium alpinum*, *Chamaedaphne calyculata*, *Cornus canadensis*, *Cystopteris fragilis*, *Dryopteris fragrans*, *Festuca saximontana*, *Glyceria striata*, *Parnassia* sp., *Poa nemoralis*, *Polypodium virginianum*, *Ribes glandosum*, *R. oxyacanthoides*, *Salix planifolia*, *Senecio pauperculus*, *Solidago graminifolia*, *Taraxacum ceratophorum.*

A.4 *Geocaulon lividum*, *Trientalis borealis.*

B.1 **Saxifraga aizoon*, *Allium schoenoprasum*, *Amelanchier bartramiana*, *Anaphalis margaritacea*, *Anemone multifida*, *A. parviflora*, *Athyrium filix-femina*, *Carex capillaris*, *C. garberi*, *Cornus canadensis*, *C. stolonifera*, *Cerastium alpinum*, *Cystopteris fragilis*, *Draba arabisans*, *Dryopteris fragrans*, *Festuca brachyphylla*, *Geocaulon lividum*, *Lycopodium annotinum* var. *pungens*, *Myrica gale*, *Oryzopsis pungens*, *Poa nemoralis*, *Polypodium virginianum*, *Ribes oxyacanthoides*, *Rosa acicularis*, *Rubus* sp., *Saxifraga tricuspidata*, *Selaginella selaginiodes*, *Solidago graminifolia*, *Taraxacum ceratophorum*, *Tofieldia glutinosa*, *Viburnum edule*, *Viola adunca.*

B.2 **Anemone parviflora*, **Carex capillaris*, *C. scirpoidea*, **Draba arabisans*, **Dryas integrifolia*, **Myrica gale*, *Agrostis scabra*, *Allium schoenoprasum*, *Andromeda glaucophylla*, *Antennaria* sp., *Anemone multifida*, *Carex eburnea*, *C. media*, *Drosera rotundifolia*, *Euphrasia hudsoniana*, *Saxifraga aizoon*, *Thuja occidentalis*, *Tofieldia glutinosa*, *T. pusilla*, *Trientalis borealis*, *Viburnum edule.*

B.3 **Andromeda glaucophylla*, **Ledum groenlandicum*, *Athyrium filix-femina*, *Calamagrostis inexpansa*, *Carex canescens*, *Drosera rotundifolia*, *Euphrasia hudsoniana*, *Festuca saximontana*, *Gymnocarpium dryopteris*, *Lysimachia thyrsiflora*, *Rubus strigosus*, *Tofieldia pusilla.*

presence of characteristic species. Attention was focussed on those species occurring in one-third to two-thirds of each set of stands from a particular type of site; species occurring in most or in few stands were considered only at a late stage of analysis. Species found in stands placed in classes A and B are listed in Table 4. The following is a synopsis of the classification.

CLASS A. Chiefly bare rock surfaces with shallow crevices only; no pools of permanent water. (4 subclasses)

CLASS B. Broken rock surfaces with wide crevices and depressions sometimes several metres square, containing pools of more or less permanent water; also including sites where rectangular blocks weather out to form a step-like shoreline with broad ledges separated by intervening vertical rises. (3 subclasses)

CLASS C. Areas of gravel, sand and coarse-grained soil often marginal to boreal, coniferous forest; along lakeshores or adjacent to other arctic-alpine communities. (3 subclasses)

CLASS D. Steep to vertical sites with a diverse range of rock types and landforms; solid rock at surface, soils and vegetation limited to crevices and narrow ledges.

CLASS E. Moderately steep talus slopes consisting of broken, angular rock fragments; soil development very limited and confined to interstitial crevices between rock fragments or to flatter tops of larger and more stable talus. (2 subclasses)

DESCRIPTIONS OF VEGETATION

A.1. *Arabis-Sagina* rock herbfield.

STRUCTURE: Chiefly bare rock with few herbs and grasses (hemicryptophytes) confined to shallow crevices.

DISTRIBUTION: This type of vegetation occurs along the north shore on the most exposed and wave-swept sites, e.g., the southern flanks of the islands between Rossport and Thunder Bay.

COMMENTS: It is a very sparse, open vegetation only found close to water level where smooth, glacially scoured, virtually featureless rock platforms gently dip into the water (Figure 5). During summer these platforms are constantly wave-washed and in winter are subject to shearing by ice. Generally, *Arabis-Sagina* communities are replaced a few metres from the lake by floristically richer ones.

A.2. *Saxifraga tricuspidata* rock herbfield

STRUCTURE: Very open stands of isolated grasses and herbs (dominantly chamaephytes and hemicrytophytes) with up to 80% rock surface covered with crustose lichens.

DISTRIBUTION: This type is seen on exposed flanks of islands between Hawk Island and Tunnel Island along the southeastern coast of Black Bay Peninsula. Occasionally it occurs on the adjacent mainland where headlands are swept by waves from the open lake. Similar communities probably occur on Isle Royale where *Saxifraga tricuspidata* also grows.

COMMENTS: This community seems to be restricted to coasts where diabase sills crop out to form almost level shore platforms. Except for one site north of Lasher Island, the number of species was low in all stands sampled, ranging from three to nine. *Saxifraga tricuspidata* herbfield sometimes forms a shoreline mosaic with heath and *Sagina*-rich stands. *Saxifraga tricuspidata* and *Festuca brachyphylla* are virtually confined to this type of vegetation.

A.3. *Potentilla-Sagina* rock herbfield

STRUCTURE: Chiefly bare rock or with a cover of crustose lichens, with scattered herbs (chiefly hemicryptophytes). In deeper crevices and less exposed parts of rock platforms are occasional stunted boreal shrubs and trees.

Fig. 5. Sequence of rock herbfield (A.1, A.3) and rock heath (A.4) on Lasher Island, Black Bay Peninsula. (Sequence runs from left to right.)

DISTRIBUTION: This type is relatively widespread along the northern shore of Lake Superior from near Batchawana Bay to Sibley Peninsula. Similar vegetation probably occurs at some locations farther west along the Minnesota section of the lake and on Isle Royale and Moose Island.

COMMENTS: Some fifty species were recorded in seven stands placed here, yet only five species occurred in four or more and over half were recorded at only one site. Although the stands are similar in structure, they differ greatly in details of floristic composition. This may be a reflection of the range of site exposures and rock types on which the stands occurred. It is the only rock herbfield noted to occur along the eastern section of the lake south of Michipicoten and parts of both Hosie's (1938) and Soper and Maycock's (1963) assemblages are referable to it. At other sites (notably McDonald Islands and islets of the Leadman group) it is the dominant vegetation close to nesting areas of shoreline birds (Figure 5).

A.4. Empetrum rock heath

STRUCTURE: Closed or sometimes more open stands dominated by woody or semi-woody carpet-forming subshrubs (chamaephytes) rooted in shallow crevices but spreading out over adjacent massive rock surfaces, sometimes with a very thin, peaty, featureless soil.

DISTRIBUTION: This often forms a discontinuous zone between rock herbfield and forest or shrubland on higher ground farther from the lake (Figure 5). It sometimes merges into "krumholz" at the edge of taller coniferous forest. Although widely distributed along the north shore of Lake Superior and locally around southern parts of the lake, *Empetrum* heath is usually of limited occurrence at any one locality (Figure 6).

COMMENTS: Similar communities occur on cobble beaches and it has been suggested that these are seral stages in a succession from open herbfield to closed coniferous forest.

B.1. Saxifraga-Arctostaphylos rock-pool herbfield

STRUCTURE: Chiefly bare or lichen-covered rock platforms, moderately to very exposed with numerous crevices and splashpools. Crevices with scattered herbs (chiefly chamaephytes and hemicryptophytes) and mat plants. Stunted trees and shrubs are occasionnally found in sheltered depressions (Figure 7).

DISTRIBUTION: This is the most widespread of the splashpool communities and best developed on the diabases and basalts of Black Bay Peninsula and neighbouring islands. These rocks have a particularly suitable structure for development of pools and depressions. Along the northeastern shore of the lake, scattered stands of arctic-alpine vegetation occur of the general type described by Soper and Maycock (1963) and by Soper (1963). These generally belong here and are well developed along the south side of Old Woman Bay, at Pointe aux Mines and at Mamainse Point. Some of the Minnesota sites briefly referred to by Butters and Abbe (1953) and Schuster (1957, 1958a, 1958b) should belong here, although we have no detailed descriptions of specific stands.

Fig. 6. Mosaic of rock herbfield (A.3) and rock heath (A.4) on Lasher Island, Black Bay Peninsula.

Fig. 7. Rock pool herbfield (B.1) on Macoun Island, Black Bay Peninsula.

A more varied range of habitats is provided in stands placed here than in those chararcterized by *Sagina* and *Scirpus*. They are generally more broken in topography with a range of habitats from xeric to mesic and from exposed to sheltered. Boreal forest species assume a greater importance with a corresponding reduction in both the number and frequency of arctic-alpine plants. Soil conditions adjacent to permanent pools are undoubtedly acidic; soil is peaty and featureless with no effective drainage. This allows species of acidic sites such as *Empetrum nigrum*, *Vaccinium uliginosum*, *Ledum groenlandicum* and *Chamaedaphne calyculata* to flourish. These less basic enclaves correspond to Schuster's "Calciphobe" *Gymnocolea-Cephalozia bicuspidata* Associule even though surrounding rocks may not be acidic. It includes, in part, Schuster's "Basiphile" *Scapania degenii-irrigua-Odontoschisma macounii* Associule defined on the basis of the lichen flora (Schuster, 1957). He pointed out that this associule of the pioneer rock-pool community occurs on basic rocks (basalts, diorites, shales and sandstones) and is sharply characterized by vascular plants such as *Primula mistassinica*, *Polygonum viviparum*, *Selaginella selaginoides*, *Potentilla fruticosa*, *Pinguicula vulgaris*, occasionally *Euphrasia hudsoniana* and *Houstonia ciliolata*, *Aster ptarmicoides* but especially *Scirpus cespitosus*. Around more or less permanent pools, which are replenished by both seepage and wave-wash, greater shelter and thin, peaty, azonal soils allow several species to persist. Boreal forest shrubs and stunted trees occur in these communities but rarely exceed a meter in height; where they rise above the surrounding shelter, branches are commonly sheared off so that they assume a layering form similar to that characteristic of "krumholz" in alpine regions. Rock-pool communities merge into one another and the division adopted here is somewhat arbitrary. Although rock-pool stands can be divided into major community groups on the basis of presence and absence of prominent species, there is some overlap and intermediate or non-conforming stands were encountered by us.

B.2. Carex-Sagina rock-pool herbfield

STRUCTURE: Chiefly bare rock with numerous clefts and small splash pools around which grow scattered herbs, grasses and occasional stunted shrubs and trees. Hemicryptophytes are prominent, but nanophytes are sometimes present in significant numbers.

DISTRIBUTION: This type was only recorded from the Slate Islands, especially where metavolcanics crop out on exposed headlands and islets.

COMMENTS: Stands placed here are characterized by relatively high proportions of arctic-alpine species. *Dryas integrifolia* is confined to this type of vegetation and *Arabis lyrata* is more common than elsewhere. Typically, *Carex-Sagina* communities are found on highly contorted rocks weathering very unevenly to give irregular surfaces pocked with numerous rough depressions and crevices.

B.3. *Calamagrostis-Ledum* rock-pool herbfield/shrubbery

STRUCTURE: Bare ground can account for as much as 90% of the surface area but often mat-forming plants are prominent. Hemicryptophytes and chamaepytes dominate but a significnt contribution comes from shrubs and low-growing trees with development of small trees or shrubbery in sheltered mesic niches especially near permanent pools. These are associated with moss hummocks and thin peaty azonal soils.

DISTRIBUTION: Four sample sites form a group regardless of the algorithm used in the analysis. Three are on Pic Island (at the northeastern and southeastern extremities) and the other is on the north end of Perley Island. Other stands occur between Pic Island and Black Bay Peninsula.

COMMENTS: Generally, shoreline communities on Pic Island were found to be floristically poorer than those on similar sites elsewhere (e.g., the

Fig. 8. Rock pool herbfield (B.3) on Pic Island. (Showing broad slabs of rock typical of sites on this island.)

Slate Islands and the islands west of Rossport). Whether this is due to the chemical or physical nature of the shoreline rocks is not known. Rock types found at Pic Island and the adjacent mainland weather to give relatively few crevices and are generally more massive in structure than types found elsewhere along the north shore of the lake (Figure 8). At Perley Island, lack of arctic-alpine species reflects a greater degree of shelter from prevailing weather. The site is marked by the prominence of boreal coniferous forest plants, although an unexpected record was *Euphrasia hudsoniana* which is frequent at the edge of the rock-pools.

A characteristic of the sites grouped here is that crevices are generally few but large with development of wide sheltered depressions containing more or less permanent splash pools surrounded by hummocks of peat. Shrubbery is found in these depressions and there is a virtual absence of the more spectacular arctic disjuncts such as *Polygonum viviparum*, *Dryas integrifolia*, *Anemone* spp., and *Sagina nodosa*. Apart from a site at François Island (in the Slate Islands) where *Festuca brachyphylla* was recorded, the only arctic-alpine species occurring in herbfield shrubbery are wide ranging species with wide ecological amplitudes.

C.1. Transitional herbfield/shrubbery

STRUCTURE: Herbs predominate although generally they are beneath or interspersed with thickets of shrubs and low-growing trees. The latter are derived from the surrounding forest and grow on markedly deeper soils showing separation into distinct A_0, A_1 and B horizons.

COMPOSITION AND SPECIES: The flora varies considerably from site to site with species largely contributed from surrounding communities. The four stands described below are representative of those seen.

(a) Barnard Point, western Mortimer Island, Slate Islands. — This site is between the west-facing, gently-sloping (10°) gravel beach exposed to moderately heavy wave action and the steep wooded slopes. The upper soil horizons are fibrous and black, the lower horizons gritty and grading into coarse beach gravels. Most abundant plants are *Linnaea borealis*, *Mitella nuda*, *Trisetum spicatum* and *Rubus strigosus*. Other species are the arctic-alpine *Lycopodium selago*, *Polygonum viviparum* and *Saxifraga aizoon*; and *Arctostaphylos uva-ursi*, *Athyrium filix-femina*, *Carex eburnea*, *Galium* sp., *Lycopodium clavatum*, *Ribes lacustre* and *Solidago randii*. Seedling and stunted juveniles (up to about one metre high) of the following forest trees and shrubs are scattered through the stand: *Abies balsamea*, *Acer spicatum*, *Alnus crispa*, *Betula papyrifera*, *Picea glauca*, *Sorbus docora*. Not recorded from this site but present in nearby similar vegetation are *Primula mistassinica* and *Taraxacum ceratophorum*.

(b) De Laute Island, northeast part of the Slate Islands. — This site is between the northeast-facing, gently-sloping (10°) metavolcanic coastal rock platform, exposed to wave action and the boreal coniferous forest. The soil is confined to crevices but increases in thickness towards the edge of the forest. Species recorded are *Arctostaphylos uva-ursi*, *Cornus canadensis*, *Empetrum nigrum*, *Ledum groenlandicum*, *Linnaea borealis*, *Lycopodium annotinum* var. *acrifolium*, *L. clavatum*, *L. obscurum*, *Trientalis borealis*, *Vaccinium vitis-idaea* and *Viburnum edule*. Scattered stunted juveniles of *Abies balsamea*, *Betula papyrifera* and *Sorbus decora* occur in the shelter of deeper crevices and where the community grades into forest.

(c) Northeast corner of Pic Island. — The site is on turf developed on zonal soil (A_0 and A_1 of silty peat, B and C of gravel and rock chips overlying solid rock) between a coastal rock platform of syenite and the forest. There is rock herbfield between the stand and the water's edge. The site is sheltered, forming a swale behind higher portions of the shoreline platform. Species present are *Amelanchier bartramiana*, *Calamagrostis inexpansa*, *Carex aquatilis*, *C. media*, *C. paupercula* var. *irrigua*, *Polygonum viviparum*, *Primula mistassinica* and *Vaccinium ulginosum*.

(d) White Lake, north of the bridge on Highway No. 17. — This is a strand vegetation along the lakeshore, generally moderately sheltered by the boreal coniferous forest behind it. The soil is chiefly gravel with interstitial silt and occasional lenses of dark fibrous peat overlying boulders and gravel derived from basement quartzo-felspathic

schist and gneiss. Bare ground accounts for 50% of the surface, the rest being herbfield with scattered thickets of shrubs. The chief species are *Triglochin palustris*, *Equisetum sylvaticum* and *Primula mistassinica*. Also recorded were *Corallorhiza trifida*, *Equisetum variegatum*, *Iris versicolor*, *Potentilla palustris*, *Salix bebbiana*, *S. candida*, *S. lucida* and *S. petiolaris*.

DISTRIBUTION AND COMMENTS: Transitional stands frequently occur adjacent to other types of arctic-alpine vegetation, connecting them with strictly boreal (usually forest) communities. Strand vegetation, such as that described for White Lake, may be regarded as a "low grade" arctic-alpine vegetation type in which the microhabitat is suitable and lack of competition is sufficient to allow species such as *Primula mistassinica* to survive. Some such stands are likely to be ephemeral; with the genesis of more fertile soils they will be invaded increasingly by progeny of trees and shrubs growing in the adjacent forest.

C.2. Sand beach and dune herbfield/grassland

STRUCTURE: Unstable, somewhat ephemeral habitats of more or less unconsolidated sand, often forming dunes; wet to dry; stability increasing away from immediate shoreline. The ground is chiefly bare except in damp hollows. Herbs and grasses predominate with local areas of mat-forming shrubs (chamaephytes and nanophanerophytes).

SPECIES COMPOSITION: This is highly variable. Species frequently encountered include *Agropyron trachycaulum*, *Ammophila breviligulata*, *Arabis lyrata*, *Artemisia* spp., *Deschampsia flexuosa*, *Equisetum arvense*, *Hudsonia tomentosa*, *Juniperus communis* var. *depressa*, *Lathyrus japonicus* var. *glaber*, *Oenothera* spp., *Polygonella articulata*, *Prunus* spp., *Smilacina stellata* and *Solidago* spp. Other plants found, especially on low dunes and in moist depressions behind protective foredunes, are *Agropyron repens*, *Andropogon scoparius*, *Anthoxanthum odoratum*, *Apocynum androsaemifolium*, *Arctostaphylos uva-ursi*, *Aster* spp., *Carex pensylvanica*, *Castilleja septentrionalis*, *Cirsium pitcheri*, *Chenopodium album*, *Comandra richardsiana*, *Corispermum hyssopifolium*, *Elymus canadensis*, *Equisetum laevigatum*, *Festuca saximontana*, *Fragaria virginiana*, *Hieracium canadense*, *H. florentinum*, *Juniperus horizontalis*, *Lithospermum croceum*, *Lycopodium tristachyum*, *Melilotus alba*, *Melampyrum lineare*, *Poa compressa*, *Salix* spp., and *Vaccinium angustifolium*. Arctic-alpine species found on sand dunes are *Elymus mollis* (Chapel Beach to Whitefish Point in Michigan, and along the northern shores of Lake Superior to Sibley Peninsula), *Stellaria crassifolia* (one record for Michigan) and *Tanacetum huronense* (southeastern corner of the lake). *Calamagrostis stricta* is recorded from Eagle Harbor (Voss, 1972).

Inland from the active dunes is a zone grading into forest which contains many boreal species including *Aralia nudicaulis*, *Coptis groenlandica*, *Cornus canadensis*, *Maianthemum canadense* and *Trientalis borealis*. Scattered individuals of forest trees (*Pinus* spp., *Abies balsamea*, *Tsuga canadensis* and *Picea glauca*) are common in this zone.

DISTRIBUTION: Beaches are scattered throughout the Lake Superior shoreline but are most frequent where younger or sedimentary rocks crop out, or where major rivers enter the lake. From Agawa Bay south to Sault Ste. Marie and along much of the south side of the lake they are scattered, but between the Pictured Rocks and St. Mary's River the stretches of sandy shore form almost one continuous beach. Along the remainder of the northern shoreline, beaches are less frequent, being best developed at the mouth of the Pic River and at Heron Bay, Sibley Peninsula and near Thunder Bay.

C.3. Bog herbfield/grassland/sedgeland

STRUCTURE: Herbs and low, prostrate or trailing shrubs predominate, usually on water-logged sandy or clay substrate or in sphagnum mats or cedar swamps. Many of the prominent species are found in adjacent coniferous forest, which is often dense, the ground cover being sphagnum hummocks and depressions with a scattering of herbs and trailing shrubs.

CHIEF SPECIES: *Chamaedaphne calyculata*, *Cornus canadensis*, *Gaultheria hispidula*, *Ledum groenlandicum*, *Petasites palmatus*, *Smilacina trifolia*, *Vaccinium oxycoccus*, *V. vitis-idaea* and *Viburnum edule* are usually present.

OTHER SPECIES: *Calamagrostis canadensis*, *Carex trisperma*, *Equisetum scirpodes*, *E. sylvaticum*, *Habenaria hyperborea*, *H. obtusata*, *Kalmia*

polifolia, *Linnaea borealis*, *Listera cordata*, *Lonicera involucrata*, *L. oblongifolia*, *Maianthemum canadense*, *Mitella nuda*, *Salix myrtillifolia*, *Scirpus hudsonianus*, *Senecio congestus* and *Trientalis borealis*. The forest trees include *Abies balsamea*, *Larix laricina*, *Picea glauca*, *P. mariana* and *Thuja occidentalis*.

DISTRIBUTION: This type of vegetation is well developed along the north shore of Lake Superior from Marathon westward and has been seen at a number of locations, including Prairie River, Jackfish River, Schreiber, Nipigon, Sibley Peninsula and Pine Bay.

Most of the species occurring in these communities are boreal or circumpolar in distribution. *Vaccinium vitis-idaea* has intermediate stations between Lake Superior and Hudson Bay, chiefly along the main river systems which flow towards the Arctic. Another arctic-alpine species to be expected in these communities is *Ranunculus lapponicus*. It has been collected at several locations along the north shore of Lake Superior but was not seen there by the authors.

D.1. Cliff herbfield

STRUCTURE: Herbs or occasional prostrate and trailing shrubs (rarely stunted tree species), confined to crevices and ledges with bare rock generally exceeding 90% coverage. Where the rock is massive and not rapidly eroded, lichens often cover much of its surface.

CHIEF SPECIES: *Cystopteris fragilis*, *Saxifraga aizoon*, *Woodsia glabella* and *W. ilvensis* are among the most frequent species encountered in cliff communities containing arctic-alpine species. *Achillea millefolium*, *Artemisia campestris* and *Cryptogramma stelleri* were found in about one third of the sites examined.

OTHER SPECIES: *Abies balsamea* (stunted), *Amelanchier sanguinea*, *Arnica lonchophylla*, *Calamagrostis purpurascens*, *Campanula rotundifolia*, *Diervilla lonicera*, *Draba hirta*, *Dryopteris fragrans*, *Fragaria virginiana*, *Hedysarum alpinum*, *Juniperus horizontalis*, *Lycopodium annotinum*, *L. selago*, *Mitella nuda*, *Pinguicula vulgaris*, *Poa glauca*, *Polygonum viviparum*, *Potentilla norvegica*, *P. tridentata*, *Primula mistassinica*, *Saxifraga tricuspidata*, *S. virginiensis*, *Shepherdia canadensis*, *Solidago randii*, *Trisetum spicatum* and *Woodsia alpina*.

DISTRIBUTION: This type of vegetation is common where diabase sills crop out along the exposed coast between Rossport and Sibley Peninsula and in areas with considerable thicknesses of low-grade meta-sedimentary rocks as on the Slate Islands and in northeastern Minnesota and adjacent Ontario. Elsewhere they are found along most large river valleys between Batchawana Bay and Michipicoten Harbour (Wawa), and from Pic River to Thunder Bay.

In general, cliff vegetation is not rich in arctic-alpine plants although species of *Woodsia* are virtually confined to such sites. The assemblage of plants found at any one site is largely dependent on the range of habitats of the cliff, the type of adjacent vegetation providing propagules and the local rock type. Habitat range is largely dependent on the frequency and form of ledges and crevices available for colonization and on whether or not the rock is resistant to erosion. Highly resistant rocks tend to have depauperate floras as there is only slow weathering to form soil and few crevices and ledges exist to hold whatever soil is formed. At the other extreme, few species occur on rapidly eroding cliffs (as at William Point, Slate Islands). The richest floras seem to occur on rocks breaking down to give a fertile soil, e.g. diabases and calcium-rich sediments with high base-exchange capacities. Almost all components of cliff floras come from adjacent communities, whether herbfield, shrubbery or forest, as indicated by a comparison of cliff floras with those of nearby, but different, stands. Butters and Abbe (1953) divided cliffs of northeastern Minnesota into "moist shady cliffs and cool canyon walls" and "dry sun-baked south-facing cliffs and dry cliff-tops." In Table 5 sites are arranged in order of decreasing shelter and increasingly rigourous microclimate. Exposed coastal cliffs tend to include species such as *Achillea millefolium* and *Campanula rotundifolia* whereas more sheltered inland cliffs or those close to forest (corresponding to the first category of Butters and Abbe) tend to be characterized particularly by *Woodsia glabella*, *Cryptogramma stelleri* and *Cystopteris fragilis*. Sites 51 and 33 contrast in rock type although in other respects they are similar. Site 51 is not an arctic-alpine community but is included merely for comparison. It is a rapidly eroding cliff of crumbling green schist at which only the two opportunists *Arabis lyrata* and *Artemisia campestris* were recorded. Neither species was a significant

Table 5. Cliff vegetation

SPECIES	SITE NUMBER [1]									
	← sheltered				exposed →					No. of occurrences.
	15	11	48	49	20	19	27	33	51	
Cryptogramma stelleri	+	+					1.3			3
Woodsia glabella	1.2	+	1.3	+	+					5
Saxifraga aizoon			+	1.1	+	1.3	+			5
Cystopteris fragilis	1.1	+		+			+	+		5
Woodsia ilvensis	+			+	+		+	+		5
Arnica lonchophylla				1.1						1
Trisetum spicatum					+	1.2				2
Fragaria vesca					+	1.2				2
Artemisia campestris s.l.					+	+			+	3
Achillea millefolium					+	+	+	2.2		4
Campanula rotundifolia							+	1.2		2
Draba hirta								1.2		1
Potentilla norvegica								1.2		1
Saxifraga triscuspidata								2.4		1
Total no. species	5	11	4	6	11	11	8	12	2	
% arctic-alpines	20	45	75	50	27	18	25	17	0	

Explanation of symbols in Table 5.

Estimates of ABUNDANCE/DOMINANCE for each species are given as a simple value according to the following scale:

+ sparsely or very sparsely present, cover very small
1 plentiful but of small cover value
2 very numerous or covering at least 5% of the area
3 any number of individuals covering 25-50% of the area
4 any number of individuals covering 50-75% of the area
5 covering more than 75% of the area.

The SOCIABILITY of each species is estimated on the following scale:

1 growing one in a place, i.e. singly
2 grouped or tufted
3 in troops, small patches or cushions
4 in small colonies, in extensive patches, or forming carpets
5 in great crowds

[1] Site numbers follow Appendix B with the addition of the following:

48. Steele River (48° 47′ N, 86° 53′ W): cliff north side of Hy. 17, E of the river (224 m.s.m.)
49. Cavern Lake (48° 50′ N, 88° 40′ W): cliff on edge of lake, 1.5 km E of Innes Lake (320 m.s.m.)
51. Barnard Point (48° 40′ N, 87° 04′ W): cliff facing west at western end of Mortimer Island, Slate Islands (188 m.s.m.)

contributor to ground cover. The other is a slowly eroding basalt site with plants found in prominent cracks produced by cooling; a total of twelve species was noted with *Achillea millefolium* and *Saxifraga tricuspidata* both contributing to ground cover.

E.1. *Pyrola* talus herbfield

STRUCTURE: Herbs (hemicryptophytes and chamaephytes) predominate but spreading shrubs and subshrubs are sometimes present. Ground and talus are invariably covered with a thick spongy moss mat. Sparse tree cover may form an open canopy above the talus; all sites seen are adjacent to coniferous forest.

CHIEF SPECIES: *Equisetum scirpoides*, *Pyrola grandiflora* and *Woodsia ilvensis* are the most frequent vascular species. The moss *Aulacomnium acuminatum* may provide up to 90% of the ground cover.

OTHER SPECIES: *Arenaria humifusa*, *Carex media*, *Draba* sp., *Gymnocarpium robertianum*, *Ledum groenlandicum*, *Mitella nuda*, *Polygonum viviparum*, *Salix myrtillifolia*, *S. rigida*, *Saxifraga aizoon* and *Viola palustris*.

DISTRIBUTION: *Pyrola grandiflora* communities are, so far, only known from the floors of Ouimet Canyon and the canyon north of Cavern Lake (northeast of Thunder Bay, 3 km southeast and 1 km northeast of Innes Lake, respectively - see Figure 10). At both localities arctic-alpine vegetation is discontinuous along the canyons. Examination of topographic maps and aerial photographs indicates that similar ground features occur north and west of these sites and west of Lake Nipigon

in the Obonga Lake–Ottertooth Lake–Paddon Lake region. Similar plant communities could be expected to occur in those areas.

This is one of the more interesting arctic-alpine vegetation types around Lake Superior, being the only habitat for the markedly disjunct species *Arenaria humifusa* and *Pyrola grandiflora*. A principal requirement is the presence throughout the summer of slow-melting ice beneath the talus blocks. This maintains temperatures locally which are considerably lower than those of surrounding talus slopes. *Pyrola* herbfield is strictly confined to cool, moist, generally shaded sites close to the ice.

It is more than a coincidence that several mosses which have been collected in the two canyons are also at their southern limit there for Ontario, e.g., *Aulacomnium acuminatum* (Lindb. & H. Arnell) Kindb. and *A. turgidum* (Wahlenb.) Schwaegr. Both species have been reported from a late-glacial assemblage in northwestern New York State, dated at about 12,000 years B.P. (Miller, 1973). The first of these species is arctic-alpine in distribution, the Lake Superior station being separated from nearest known sites in northwestern Canada by about 2,400 km (Williams, 1968; Vitt & Horton, 1979). Another arctic-alpine species, *Myurella tenerrima* (Brid.) Lindb., has been collected by C.E. Garton in both Ouimet Canyon and the canyon at Cavern Lake (Ireland & Trucco, 1979).

E.2. *Dryopteris-Woodsia* talus herbfield/shrubbery.

STRUCTURE: Chiefly well-spaced herbs (hemicryptophytes and chamaephytes) in the interstices between boulders, but sometimes with a significant proportion of low-growing shrubs. Lichens may account for 50–75% of the ground cover. Little soil is present.

CHIEF SPECIES: *Cystopteris fragilis*, *Dryopteris fragrans*, *Polypodium virginianum*, *Ribes lacustre*, *Rubus idaeus*, *Saxifraga aizoon*, *Woodsia ilvensis*, *Arabis divaricarpa*, *A. lyrata*, *Asplenium trichomanes*, *Celastrus scandens*, *Cornus rugosa*, *C. stolonifera*, *Draba norvegica*, *Fragaria virginiana*, *Lycopodium selago*, *Poa glauca*, *Rhus radicans* var. *rydbergii*, *Ribes glandulosum*, *Rubus strigosus*, *Saxifraga virginiensis*, *Shepherdia canadensis*, *Solidago randii*, *Trisetum spicatum*, *Viburnum edule*. Trees and shrubs noted in open talus stands and as isolated specimens or forming coppices are *Abies balsamea*, *Acer spicatum*, *Betula papyrifera*, *Sambucus pubens*, *Sorbus decora* and *Thuja occidentalis*.

DISTRIBUTION: Open debris slopes are scattered throughout the area adjacent to Lake Superior in association with cliffs and steep hillsides. Talus with arctic-alpine components is particularly well developed in association with diabase sills between Lake Nipigon and Thunder Bay and along valleys which have cut canyons, east of Nipigon. Shoreline talus is less frequent. It was sampled at the Slate Islands and on the inland side of islands flanking Black Bay Peninsula. Butters and Abbe (1953) described similar talus slopes in the Pigeon River area of northeastern Minnesota along the shores of small lakes. They recorded *Saxifraga cernua* from talus in this area.

Talus with significant numbers of arctic-alpine plants tends to be found mostly in areas where rocks weather to give angular blocks. In this unstable habitat, vegetation is virtually restricted to crevices between the blocks. *Dyropteris fragrans* and *Saxifraga aizoon* are the two most frequently encountered arctic-alpine species, becoming more common in areas where basement rocks are high in calcium. Studies of talus vegetation elsewhere show that is is frequently a seral stage in the succession towards forest. Detailed analyses were not made at Lake Superior but comparison of the descriptions and photographs in Hosie (1938) with the same sites in 1973 suggests that some talus slopes may be proceeding rapidly towards forest (Figure 9). In contrast, talus slopes in the canyon at Cavern Lake showed little sign of succession towards a closed shrub-dominated or tree-dominated cover (Figure 10).

The role of arctic-alpine taxa. — Surprisingly few arctic-alpine species occur in a wide range of communities: approximately 55% for which we have habitat information are restricted to one type of community. Only 16% occur in five or more, with *Trisetum spicatum* in eight; *Poa glauca*, *Polygonum viviparum*, *Primula mistassinica* and *Saxifraga aizoon* in six; and *Empetrum nigrum* and *Pinguicula vulgaris* in five. In many instances, arctic-alpine species, though present, play only a minor role. Just over 30% of the species for which we have data play a definitive role in a particular community and can be regarded as major species.

Fig. 9. Rock talus and cliffs above Carp Lake, Batchawana Bay.

The species of relatively wide ecological amplitude mentioned are widespread in occurrence around Lake Superior. For the most part they are successful in low-arctic habitats throughout their total geographic range and they may be regarded as opportunists. The relative failure at Lake Superior of some other successful arctic plants is notable. *Dryas integrifolia* and *Saxifraga cernua* are both widespread through the North American Arctic and occupy a wide variety of habitats. Yet, at Lake Superior, they are virtually confined to single localities.

If the total number of arctic-alpines for each community is considered, it shows that the greatest numbers of these species occur in rock pool habitats (B.1. to B.3.) and on cliffs (D.1.).

Fig. 10. Sheer diabase walls and talus slopes of canyon at Cavern Lake. (Arctic-alpine species are concentrated where the talus slopes meet.)

Smallest numbers are found in the rock herbfield of barren, exposed shores (A.1. to A.4.). This is a reflection of the great diversity of niches in rock pool communities and of the scattered occurrence on cliffs of "migrant" species from adjacent arctic-alpine stands. The actual numbers of species recorded from each community type are (in descending order): B.2 - 16, B.1. - 15, D.1. - 13, B.3. - 10, A.3. - 9, C.1. - 8. E.2. - 8, C.2. - 6, C.3. -5, A.2. - 4, E.1. - 4, A.4. - 2, A.1. - 1.

For *Astragalus alpinus*, *Draba aurea*, *D. incana*, *Lycopodium alpinum*, *Phleum alpinum*, *Poa alpina* and *Potentilla multifida* we have insufficient habitat information to assign each species to a class or community. All are of very limited distribution in the Lake Superior region.

DISTRIBUTION PATTERNS

The species making up the arctic-alpine element of the Lake Superior basin represent only a small proportion of the total arctic flora. Porsild (1964) listed 340 species and major geographical races of flowering plants and ferns for the Canadian Arctic Archipelago. Of these, less then 20% are known to occur at Lake Superior; for the considerably larger circumpolar Arctic flora the percentage at Lake Superior is correspondingly lower. On the other hand, some members of the arctic-alpine element at Lake Superior are strictly low-arctic species which do not extend far enough north to justify inclusion in Porsild's Flora.

In North America: In Table 1 the arctic-alpine species at Lake Superior are arranged according to their distribution within the North American Arctic, and their occurrence south of the Arctic. Subdivision of the Arctic (Figure 3) follows, with slight modifications, that of Young (1971). Although similar, it differs in detail from that suggested by Porsild (1958) on the basis of vegetation types. Zones 1-4 of Young (Extreme Arctic, High Arctic, Mid-Arctic and Low Arctic respectively) are recognized together with a Subarctic Zone (Zone 5) consisting of the taiga tundra-coniferous forest transition. Boundary changes chiefly result from an attempt to reconcile vegetation and floristic approaches to arctic zonation and from a consideration of the northern limits of abundance of individual species as well as northern limits of absolute range.

Of the arctic-alpine species at Lake Superior, the majority reach their greatest abundance in subarctic or mid-arctic zones. Only three are abundant in the extreme-arctic cold deserts of the far north. These are notably ubiquitous arctic plants occupying a wide range of habitats and reproducing under the most inhospitable conditions. High-arctic species are, however, less successful in surviving south of the Arctic. Mostly, they occur at few sites outside arctic and alpine regions. The most persistent of the arctic-alpine plants at lower latitudes are species which occur commonly in the Mid-Arctic and Low Arctic. These also are generally frequent in alpine tundra of both eastern and western North America. Surprisingly, the low-arctic and sub-arctic species are, with the exception of a few such as *Calamagrostis stricta*, *Pinguicula vulgaris*, *Ranunculus lapponicus* and *Primula mistassinica*, consistently poor performers south of the Arctic. A substantial number have their distribution centred on the tundra-coniferous forest interface, extending generally only a short distance north into the Arctic or south into the continuous forest.

Of the lowland southern outliers (Table 1), that centred on the Gulf of St. Lawrence is the richest in Lake Superior arctic-alpine species. This region, and particularly the Gaspé Peninsula, has long been known to have a remarkably high number of spectacular disjuncts and plants of arctic-alpine affinity (Fernald, 1925; Scoggan, 1950; Drury, 1969). However, typically arctic species such as *Cassiope hypnoides*, *Rhododendron lapponicum* and *Oxyria digyna* which occur at the Gaspé Peninsula are absent from the Lake Superior basin although the *Rhododendron* occurs just to the south in the Driftless Area. Fernald (1925, 1935) explained these disjunctions on the basis of persistence *in situ* of cordilleran and arctic plants throughout the Pleistocene glaciation. It is more likely that the coast of Ungava, Labrador and Newfoundland provided migration routes and refugia which, in conjunction with offshore and foreland refugia to the south, allowed a considerable number of arctic-alpine plants to reach the Gaspé Peninsula and surrounding areas in late-glacial times. These plants have subsequently been preserved in habitats similar to those in which arctic-alpine species currently occur at Lake Superior.

More than half of the arctic-alpine element at Lake Superior is recorded from south of the arctic tundra in Manitoba and over a third from similar parts of Alberta and Saskatchewan. This contrasts with boreal Ontario which has only eight arctic-alpine species in common with the study area. Most records are from cliffs, lake shores and river gorges. The Hudson Bay lowlands and Clay Belt of Ontario are relatively poor throughout in arctic species and although Baldwin (1958) listed 21 arctic and 71 "(arctic) subarctic" species for the Clay Belt, amounting to 10% of the regional flora, virtually all are widespread throughout boreal forest, prairie, or temperate regions and cannot be regarded as exclusively arctic plants.

The lower Great Lakes share with Lake Superior twenty arctic-alpine species, most of which are mid-arctic and low-arctic. Some species such as *Lycopodium selago* and *Carex scirpoidea*

occur both in tundra-like communities with non-arctic species and as isolated populations within typically boreal conferous and Great Lakes deciduous forest. At a few sites, however, particularly along exposed shorelines of lakes, distinct communites of tundra occur although these are invariably poorer in species that those found at Lake Superior. In eastern Ontario, a notable occurrence of arctic-alpine plants is known from the deep gorge of the Barron River (Brayshaw, 1964). Here *Dyopteris fragrans* and *Saxifraga aizoon* grow on cool, nearly vertical cliffs at the bottom of the gorge.

Few of the arctic-alpine taxa at Lake Superior also occur in the Driftless Area to the southwest. Descriptions of the occurrence of the disjunct northern species in the western part of the Driftless Area indicate that these involve boreal rather than arctic-alpine elements (Hartley, 1966). Few such species seem able to tolerate conditions in the region at the present day. Those that do, including *Rhododendron lapponicum*, persist only as small populations in cool habitats at isolated sites.

At Lake Superior — For only a few species have detailed distribution maps been published. These include *Tanacetum huronense* and *Elymus mollis* (Guire & Voss, 1963); *Woodsia alpina*, *Trisetum spicatum*, *Polygonum viviparum*, *Sagina nodosa* and *Saxifraga aizoon* (Soper & Maycock, 1963); *Empetrum nigrum* (Soper & Voss, 1964); and *Primula mistassinica* (Soper, Voss & Guire, 1965 and 1972). Detailed distribution maps based on herbarium records, field observations and published records indicate that the arctic-alpine element occupies a discrete part of the region but that its constituent members display a range of distribution patterns within this. Some parts of the Lake Superior basin are still imperfectly explored and significant new records will likely result from detailed examination of areas such as the shore between Marathon and Michipicoten and the valleys west of Lake Nipigon. However, records are sufficiently complete to show the generalised distribution of the arctic-alpine element which is concentrated along the northern shore of the lake from Duluth to Sault Ste. Marie, on Isle Royale and on Michipicoten Island.

Most stretches of rocky coast along the north side of the lake have assemblages of arctic-alpine plants. Best developed assemblages are generally found on rugged shores of hard rock, exposed to wave action and inclement weather, and in close proximity to deep water. Largest numbers of taxa result where topography is rugged and varied with numerous crevices, ledges and small wave-washed pools.

Away from the shore on the north side of the lake, the arctic-alpine element is usually impoverished. Several species are known from sites adjacent to the shore of Lake Nipigon but these occur in smaller numbers than at comparable sites around Lake Superior. Southwest of Lake Nipigon, tundra plants persist in the cool, moist regime of canyons and include two species (*Pyrola grandiflora* and *Arenaria humifusa*) found nowhere else in the Lake Superior basin. Along the Pigeon River and its tributaries to the south a series of enclosed valleys and lakes provides further inland habitats for arctic-alpine species, which occur there in association with cordilleran disjuncts (Butters & Abbe, 1947, 1953).

Except for the northern end of the Keweenaw Peninsula, the arctic-alpine element is poorly represented along the southern side of Lake Superior. At Keweenaw twenty arctic-alpine taxa have been recorded, their occurrence being described by Fernald (1935), Richards (1952 a & b), and Wells and Thompson (1974). The most recent of these papers draws attention to the huge masses of bare rock often lining the Lake Superior shore and the frequency of arctic-alpine and boreal plants in such locations.

Although much of the shoreline of Lake Superior and parts of its drainage system have been thoroughly examined for arctic-alpine plants, numerous areas exist for which there is little or no information. Maps and aerial photographs for the whole region indicate numerous sites which might harbour plants of northern affinity and we have identified thirty-five "first order" sites where we consider there is a high probability of discovering arctic-alpine disjunct species. The majority are located in the northwest sector of the Lake Superior basin and, although examination of them is unlikely to alter fundamentally distribution patterns known already, it is possible that new taxa will be added to the arctic-alpine element especially at sites similar to Ouimet and Cavern Lake Canyons. Chief interest centres on a canyon system west of Lake Nipigon (Obonga Lake, Pantegruel Creek, Ottertooth Lake, Paddon Lake) and on extensions to the two canyons which already have been explored.

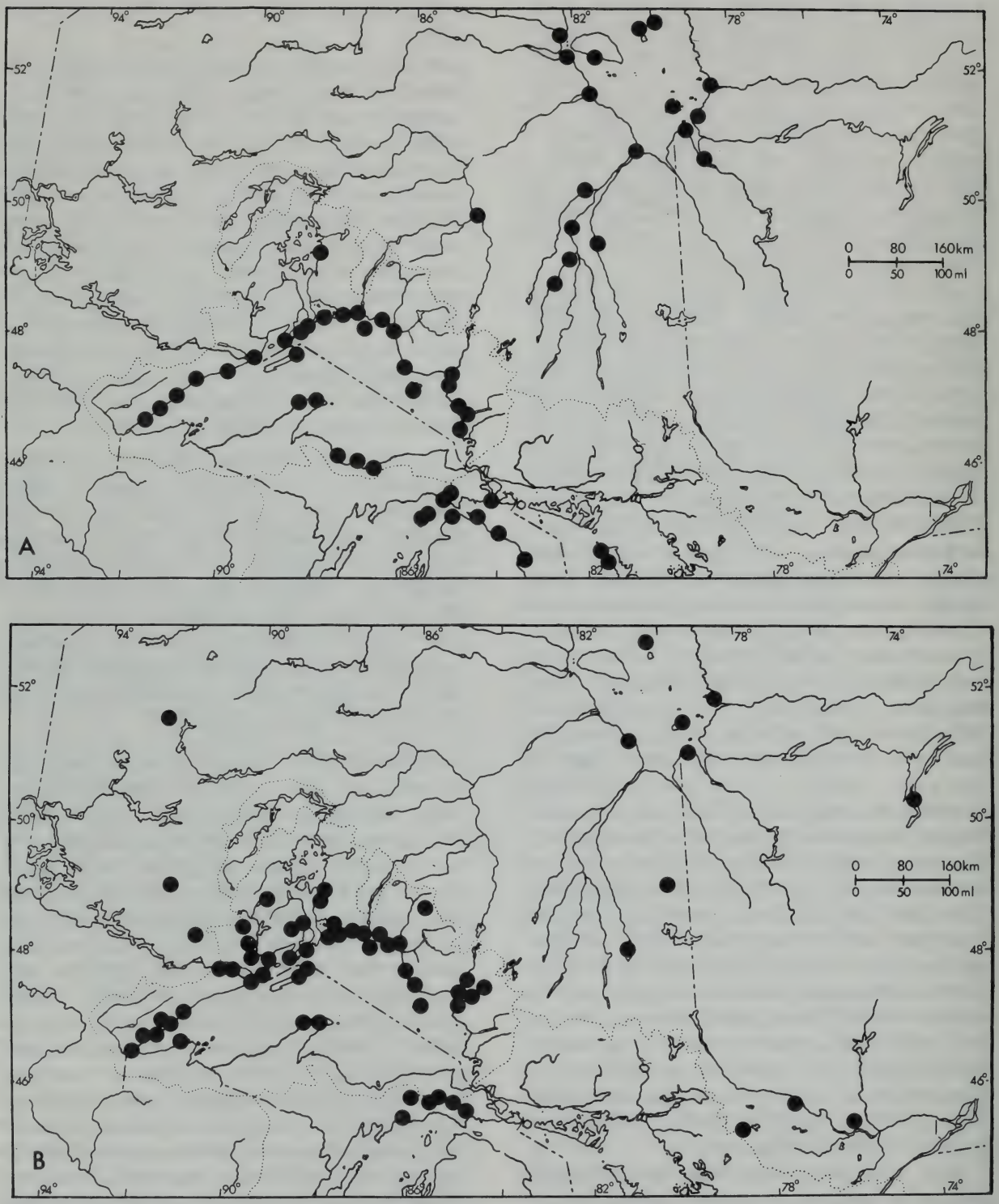

Fig. 11. Distribution of two species from Group A: A, *Pinguicula vulgaris*; B, *Lycopodium selago*.

Widely distributed species (Group A)

The nine most widespread arctic-alpine species at Lake Superior can be divided into two subgroups. *Dryopteris fragrans*, *Pinguicula vulgaris* (Figure 11A), *Poa glauca*, *Polygonum viviparum*, *Primula mistassinica*, *Scirpus cespitosus* (Figure 11B) and *Trisetum spicatum* have each been recorded from several parts of the south shore of Lake Superior as well as from numerous sites on the north shore. The remaining species, *Lycopodium selago* (Figure 12) and *Woodsia glabella* are either absent from or rare in the southern part of the Superior basin.

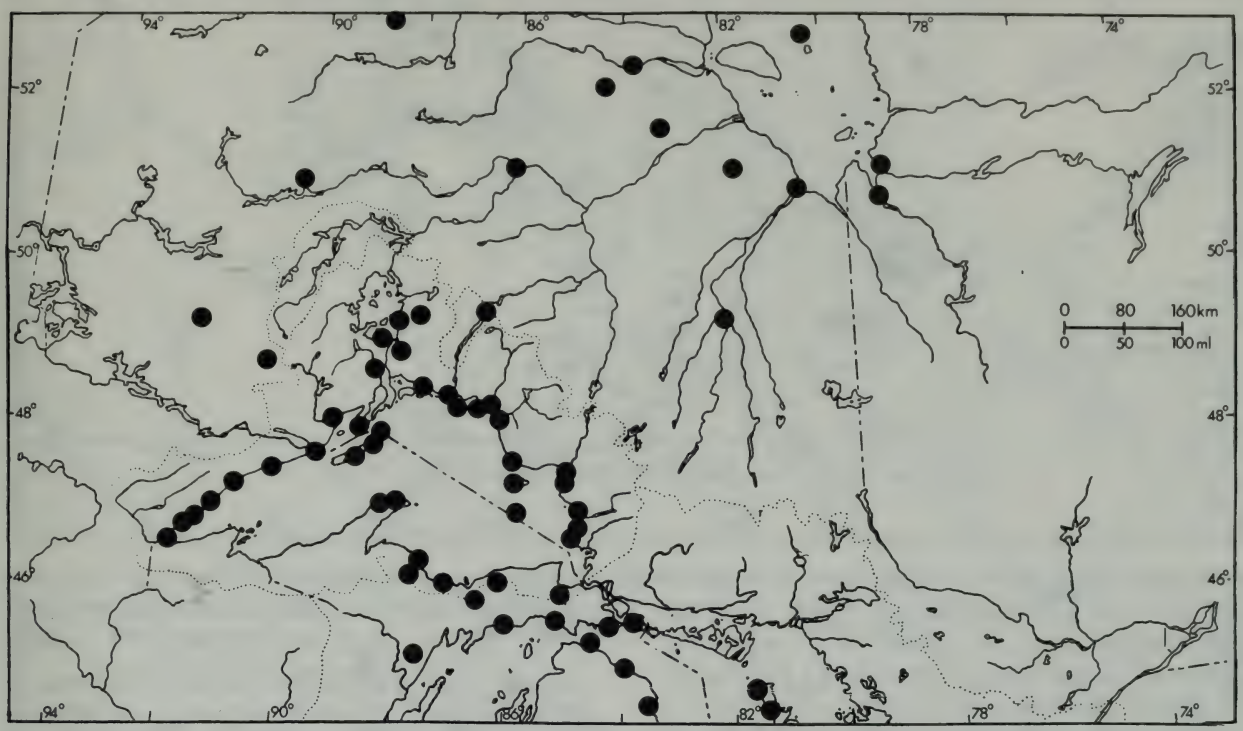

Fig. 12. Distribution of *Scirpus cespitosus*, a species from Group A.

Species with an eastern bias (Group B)

A further eight species occur from the Pigeon River to the Pic River but become more abundant towards Sault Ste. Marie at the easternmost point of the lake shore. These are *Sagina nodosa*, *Saxifraga aizoon*, *Empetrum nigrum*, *Castilleja septentrionalis* (Figure 13A), *Carex capillaris*, *Carex scirpoidea* (Figure 13B), *Elymus mollis* and *Selaginella selaginoides* (Figure 14). They are found on the south side of the lake. *Saxifraga aizoon* and *Carex scirpoidea* occur along the lake shore and on rocky slopes and cliffs away from the lake; the remainder are almost exclusively shoreline plants.

Species with a western bias (Group C)

Senecio congestus (Figure 15A) at Lake Superior occurs at a few scattered sites both inland and close to the lake from Duluth to the Lake Nipigon area. *Woodsia alpina* is chiefly a shoreline species with a similar range although also reported from near Wawa. *Euphrasia hudsoniana* (Figure 15B) is frequent from Duluth to near Pic River, and *Vaccinium vitis-idaea* has a more extensive distribution, also ranging inland to Lake Nipigon and inland in Minnesota.

Species frequent between Pigeon River and Pic River and rare or absent elsewhere (Group D)

Three species fall into this category: *Ranunculus lapponicus* (Figure 16A). *Tofieldia pusilla* (Figure 16B) and *Vaccinium uliginosum*. These characteristically occur in bogs, wet woodlands, heath and on shores.

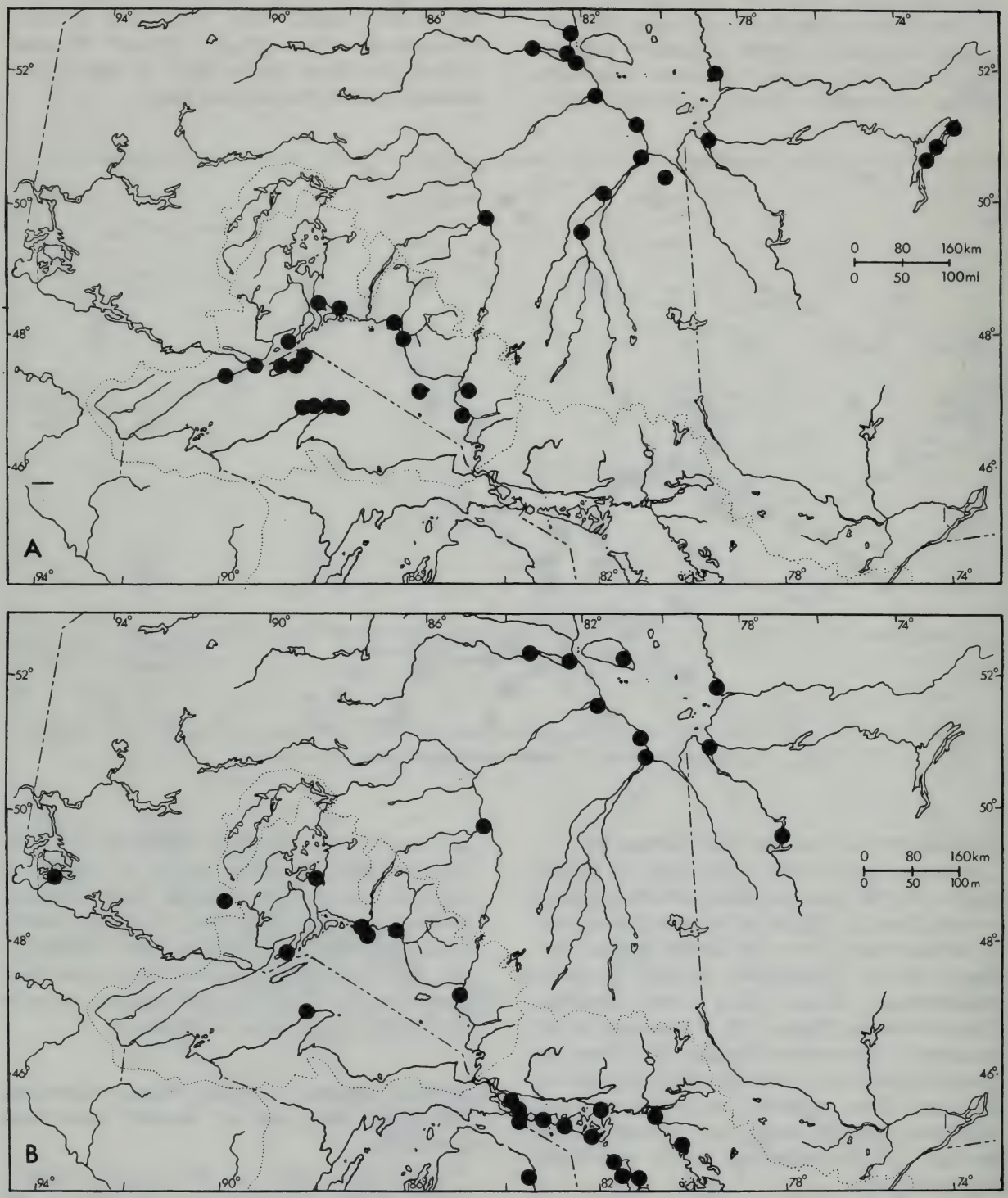

Fig. 13. Distribution of two species from Group B: A, *Castilleja septentrionalis*; B, *Carex scirpoidea*.

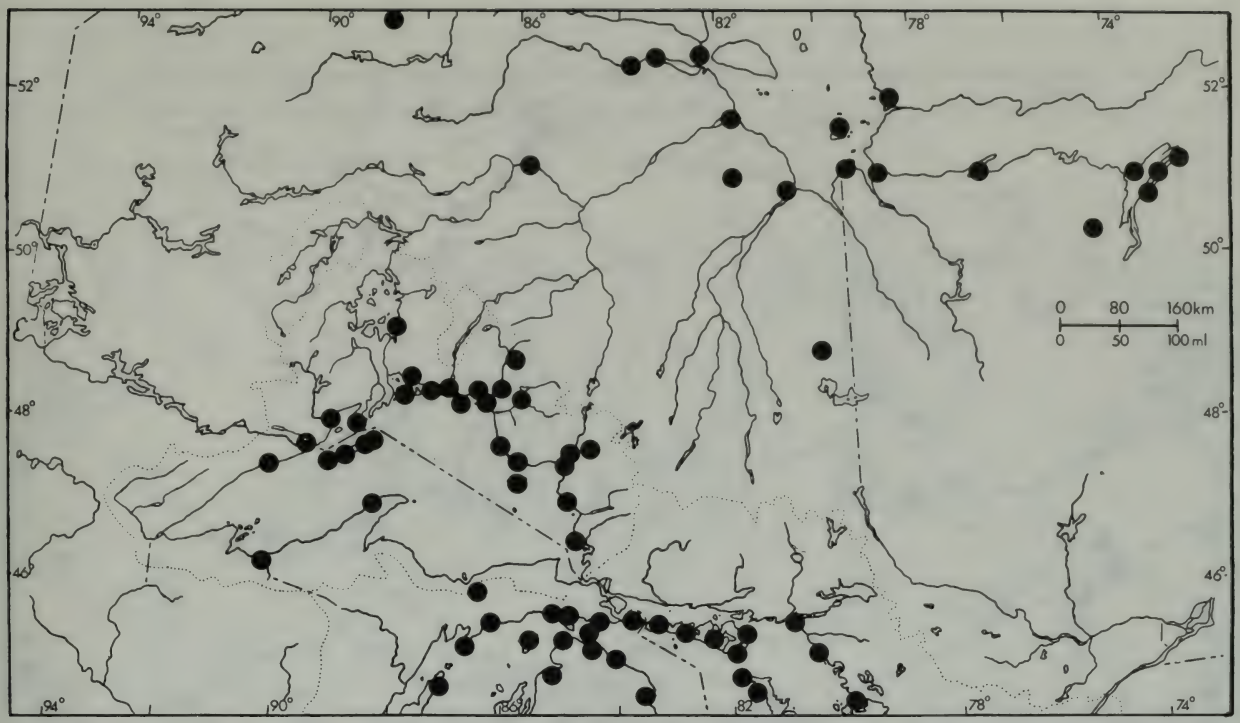

Fig. 14. Distribution of *Selaginella selaginoides*, a species from Group B.

Species uncommon and restricted to Pigeon River - Pic River (Group E)

Seventeen arctic-alpine species at Lake Superior are known from few (generally three or fewer) localities. With the exception of *Calamagrostis stricta*, which is recorded from the Keweenaw Peninsula on the south shore of the lake, all are restricted to the north shore of Lake Superior between Pigeon River and Pic River, inland to Lake Nipigon, and the northern tip of Isle Royale and associated islets. Within this area there are concentrations of these species at particular localities.

Six occur at Pigeon River (*Carex supina*, *Calamagrostis stricta*, *C. purpurascens*, *Cerastium alpinum*, *Draba norvegica* and *Saxifraga cernua*), four on Sibley Peninsula (*Calamagrostis purpurascens*, *Draba aurea*, *Hedysarum alpinum* and *Potentilla multifida*), four on the Slate Islands (*Anemone parviflora*, *Cerastium alpinum*, *Dryas integrifolia* and *Taraxacum ceratophorum*), three from canyons west of Nipigon (*Arenaria humifusa*, *Pyrola grandiflora* and *Salix myrtillifolia*) and two from Isle Royale and nearby islets (*Draba incana* and *Saxifraga tricuspidata*). The Isle Royale *Saxifraga* also extends for about 20 km along the Black Bay Peninsula and its off-shore islets where it is common on rocky exposed sites (Figure 17). Outside the areas mentioned, *Calamagrostis stricta*, *Hedysarum alpinum*, *Potentilla multifida* and *Salix myrtillifolia* occur at a few widely scattered sites.

Other species of restricted distribution (Group F)

A residue of seven species is locally distributed with distribution patterns significantly different from those already described. *Tanacetum huronense* is known on Lake Superior only from the southeastern part, where it occurs on sandy shores from Grand Marais, Michigan, to Batchawana Bay, Ontario. It occurs in the Gulf of St. Lawrence and along low-arctic and subarctic coasts. Other arctic-alpine species which are restricted on Lake Superior to the south shore include *Lycopodium alpinum* (Keweenaw Peninsula), *Phleum alpinum* (only verified for the Keweenaw Peninsula but recently reported (Anonymous, 1974) from the coast between Marathon and Michipicoten). *Poa alpina* is known from Keweenaw Peninsula, Isle Royale and the Pic River, and

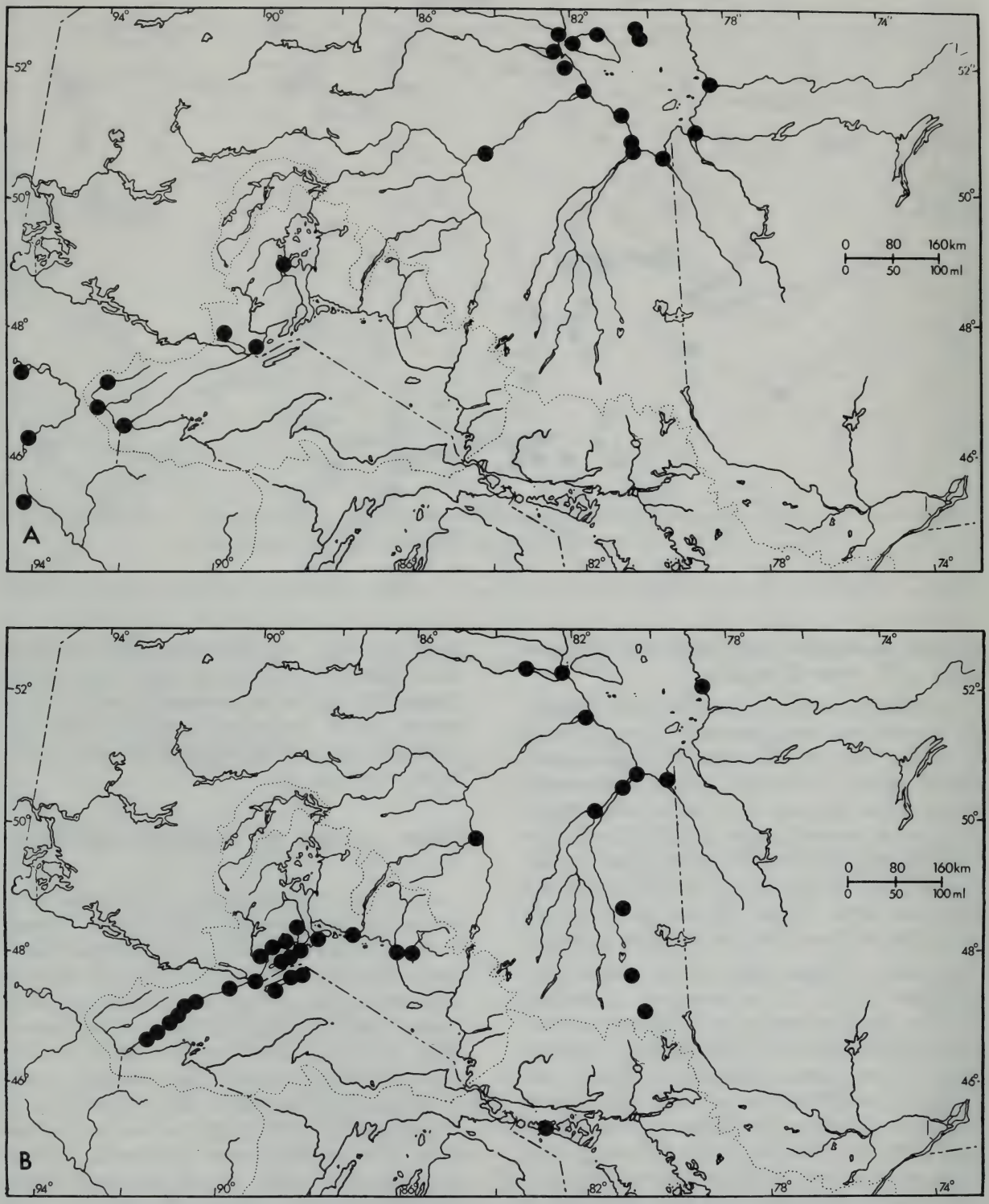

Fig. 15. Distribution of two species from Group C: A, *Senecio congestus*; B, *Euphrasia hudsoniana*.

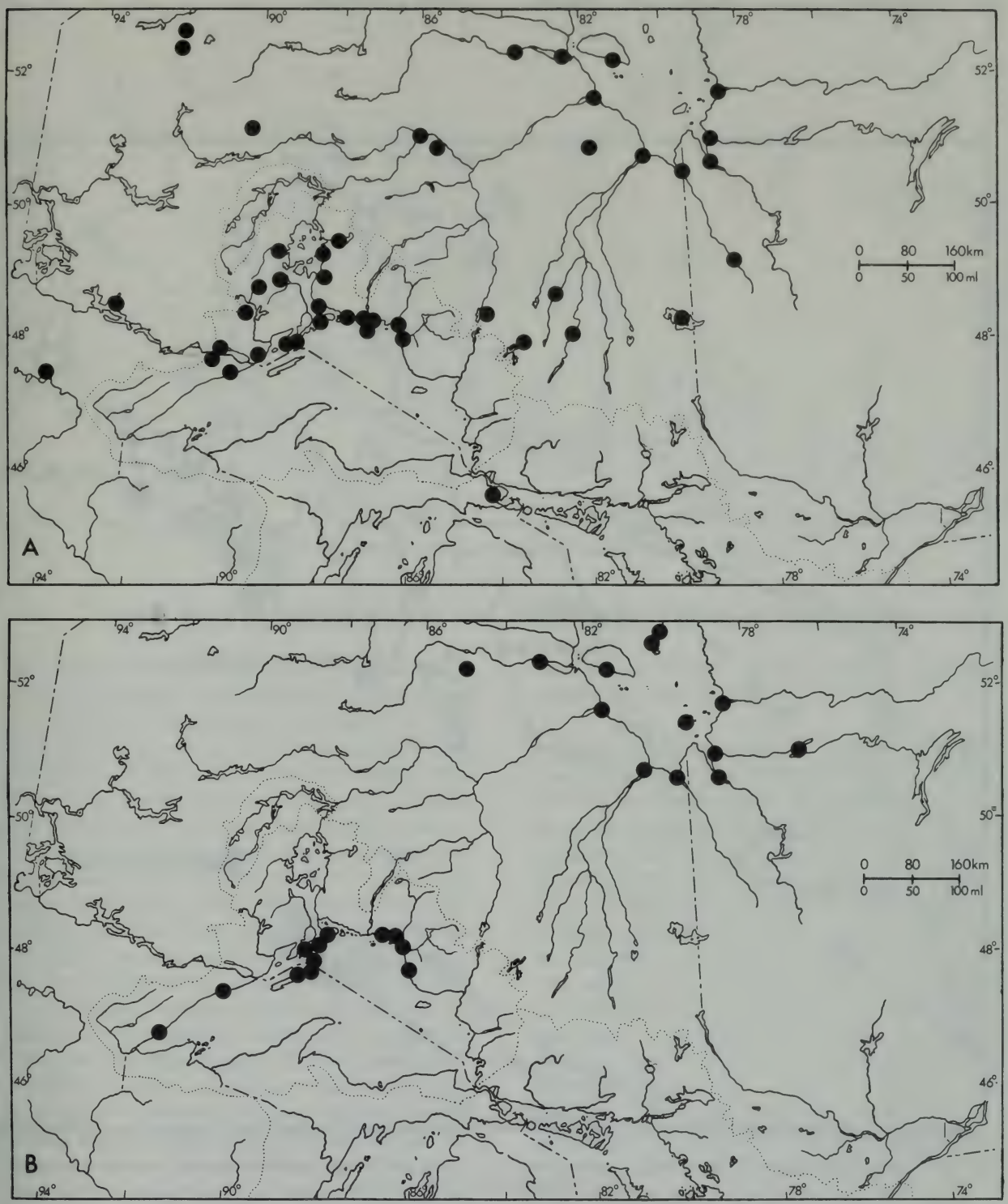

Fig. 16. Distribution of two species from Group D: A, *Ranunculus lapponicus*; B, *Tofieldia pusilla*.

Carex saxatilis from a single station at Corbeil Point on the east shore of Lake Superior (Figure 18). *Astragalus alpinus* is known from the Sibley Peninsula and Michipicoten, and *Festuca brachyphylla* occurs rarely in very exposed sites, at several localities.

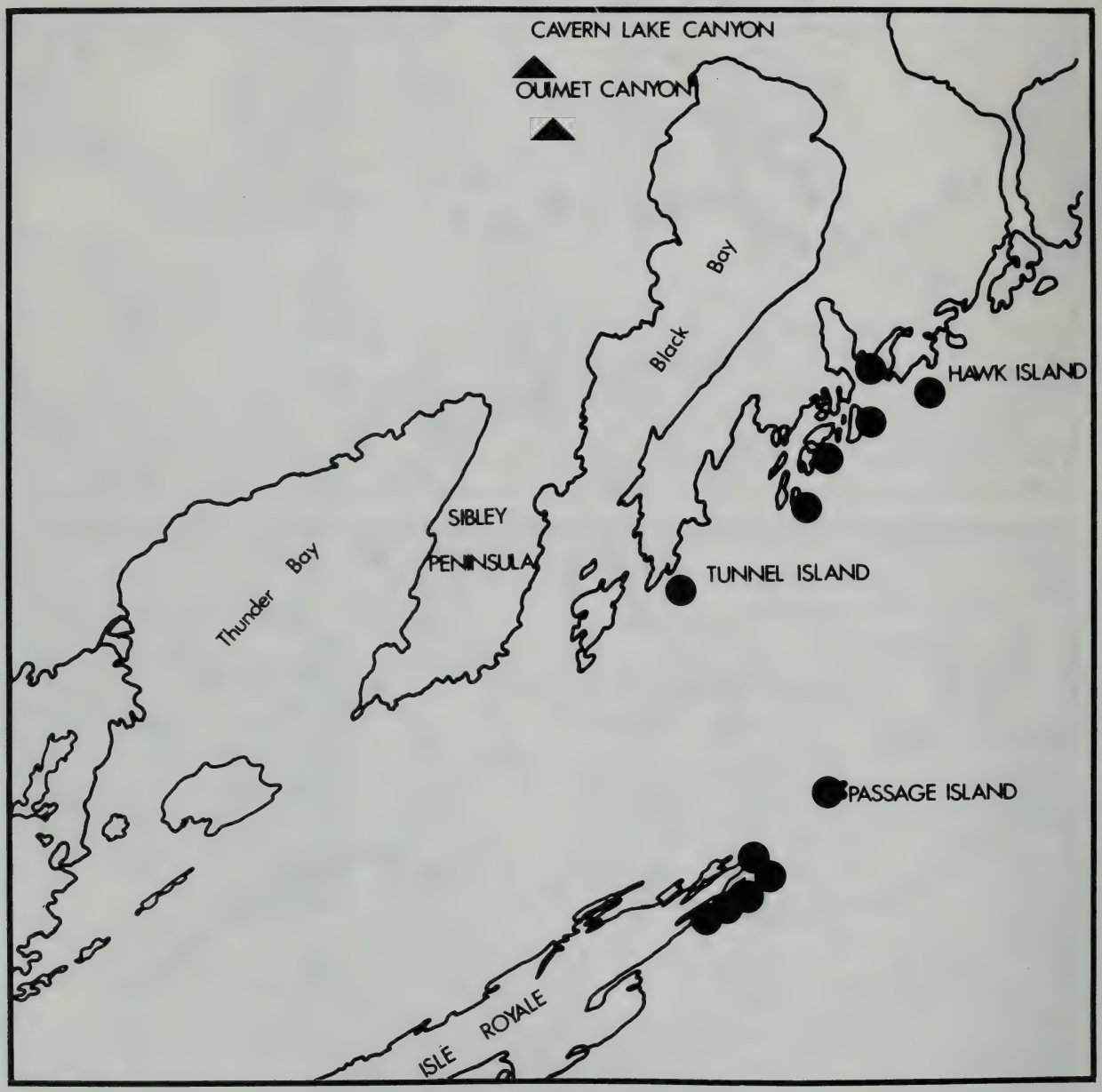

Fig. 17. Distribution at Lake Superior of *Saxifraga tricuspidata* (circles) and *Pyrola grandiflora* (triangles). *Arenaria humifusa* occurs in the canyon at Cavern Lake.

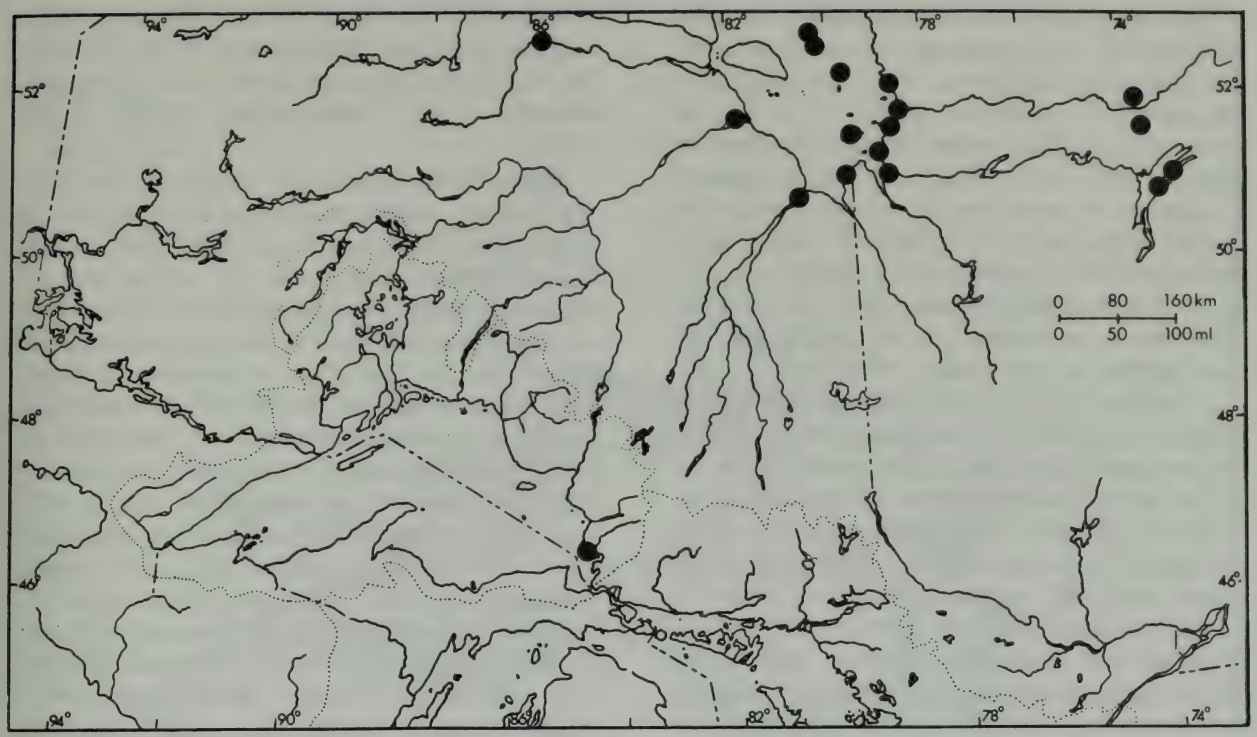

Fig. 18. Distribution of *Carex saxatilis*, a species from Group F.

THE DETERMINATION OF DISTRIBUTION PATTERNS

The distribution pattern of a particular taxon is a product of the interaction between its genome and environmental determinants, modified by the history of the species in the region. Determinants will not act in the same way on different species and at Lake Superior this is shown in the distribution patterns of different arctic-alpine species. Few appear to have identical distribution patterns. Where they do, e.g., *Arenaria humifusa* and *Pyrola grandiflora*, close examination of communities in which they occur demonstrates that although gross geographic distribution is similar, fine distribution of individual plants is not.

A particular problem is that it may not be gross features of microclimate which, in the long term, determine whether a species will or will not survive at a particular site, so much as subtle details such as length of snow-lie, windiness during certain seasons and diurnal variation in temperature. In some instances, what happens infrequently may be more critical than the normal event. For example, an occasional, but severe, drought or rare late spring frost may be the critical factor in preventing plants from becoming established at particular sites. Such information is, however, usually unavailable except where detailed long-term studies are undertaken.

Griggs (1940) has suggested that the ecology of rare plants, including outlying occurrences of cordilleran or arctic-alpine disjuncts as at Lake Superior, parallels that of many weed species. He proposed (loc. cit., p. 576) that "the difference between a rare species and a common one lies in the fact that the one fails or almost fails to establish its progeny in the competition for its habitat where the other succeeds in so doing". This assumes that rare plant habitats are unstable and that the communities they are associated with are seral, in time yielding to climax vegetation. There is little to suggest that arctic-alpine communities at Lake Superior are, as a general rule, dynamic and moving towards a climax or subclimax state, which, in this region, would be either boreal coniferous or deciduous forest. Rather, communities, particularly those of the shores of the lake, form a series of zones maintained in a static state by local pecularities of climate, geology and topography which inhibit the growth of plants that could grow taller.

It has been postulated that there are three major determinants of vegetation: competition, stress and disturbance (Grimes, 1974). Competition is the attempt by neighbouring plants to utilise the same units of light, water, mineral nutrients or space; stress is the inhibition of the development of biomass by restriction of primary production (usually imposed by shortages of water, light, mineral nutrients, suboptimal temperatures, soil and toxins) and disturbance is similar to stress but inhibition is by damage due to grazing animals, man, pathogens, soil erosion, wind, etc.

In habitats where mat-forming species such as *Empetrum nigrum* and *Vaccinium vitis-idaea* have become established, only a few other species are able to survive the competition for space and light. However, in most other types of arctic-alpine community at Lake Superior, plants are widely spaced and only within individual crevices or around the margins of rock pools is there likely to be significant competition between individuals. This is suggested by the local occurrence in herb-field shrubbery of small areas of nano-phanerophytes and macro-phanerophytes with elevated leaf canopy, extensive lateral spread and a tendency to accumulate appreciable amounts of litter. Most arctic-alpines at Lake Superior are characterised by low potential growth rates, a feature of the "stress-tolerant" strategy of Grimes (1974).

We suggest that the chief factors in maintaining arctic-alpine habitats at Lake Superior are stress and (to a lesser degree) disturbance. These prevent the permanent establishment of shrub-dominated or tree-dominated vegetation at most sites and in few instances will there be succession to vegetation more typical of the region. Any such succession is chiefly confined to the edges of beaches, stranded cobble terraces and larger, sheltered depressions at the foot of talus slopes and the rear of coastal rock platforms.

Shoreline Microclimate

Louis Agassiz was the first to suggest that the cold waters of Lake Superior were largely responsible for maintaining arctic-alpine habitats along its margin. He measured the open-lake temperature (Agassiz, 1850) as about 40°F (4.5°C) which is a little below modern measurements (Soper & Maycock, 1963). Summer surveys indicate that large areas of the lake are cold with maximum water temperatures at the surface of about 5°C. Much of the lake surface will reach maximum temperatures below 10°C even during the warmest months of July and August (Fig. 19). In contrast, the records for the other Great Lakes show considerably higher temperatures, ranging up to 18°C.

Millar (1952) isolated two factors in determining the low temperature regime of the lake. It is deeper than most other large lakes and bottom water probably remains at the temperature of maximum density throughout the whole year. He also suggested that cool surface temperatures are induced by the formation of extensive ice-sheets over much of the lake surface during winter. The central part of the lake remains free from ice at all times. Detailed studies by Ragotskie and Bratnick (1965) indicated that, in late summer, two areas of cold water dominate the surface temperature pattern, with associated minor cold water ponds peripheral to these. They proposed a model explaining the persistence of such areas as a balance between radiation heating of the surface layers and upwelling of colder water from below. Measurements of temperature profiles show that wind stress or seiche effects remove the surface layer of heated water from central parts of the lake allowing upwelling of deeper cold water (Hachey, 1952; Rodgers, 1965).

Typical mid-summer temperatures of surface water on Lake Superior appear to correlate closely with the distribution of arctic-alpine plants along the shoreline of the lake (Fig. 19). Conversely, arctic-alpine species are virtually absent from sections of the lakeshore adjacent to water reaching maximum summer temperatures at the surface in excess of 15°C.

The primary effect of low water temperatures is probably to reduce the overall summer temperature regime of nearby shores. Shitara (1969) showed that the thermal influence of a cool lake on local shore microclimate may lead to still-air temperature reductions of up to 4.5°C when the water surface temperature and still-air temperature differ by 7–9°C. This effect is most pronounced on windward shores, which at Lake Superior in summer, would be along the north and northeast sides of the lake. He demonstrated that the effect is most pronounced close to the water's edge, becoming negligible a short distance from the lake. At Lake Superior the width of the tundra-like arctic-alpine strip along the lake shore is often very narrow, rarely exceeding 20 metres in width.

Fig. 19. Distribution of arctic-alpine plants at Lake Superior with surface water temperatures. (Dots represent individual records, shaded areas indicate richest assemblages. Temperature data after Rodgers (1965) for July 18–24, 1965.)

Strommen (1969) commented on the high concentration of minimum temperatures into small ranges indicating the strong influence exerted by the cool waters of Lake Superior at Isle Royale. Minimum temperatures in June exceed 50°F (10°C) for an average of only 2 days. In July, August, and September minimum temperatures exceeding this occur on an average of 17, 25 and 10 days respectively. In association with lowering of overall temperatures is the probability of a reduced growing season. Wells and Thompson (1974) pointed out that on the Michigan shore, although westerly cold fronts may be warmed by Lake Superior waters as much as 11°C, cold winter temperatures, once achieved, persist longer into the spring due to the lag effect of the cold water. Commencement of spring near Copper Harbor on Keweenaw Peninsula may be 10–15 days later than further inland with a corresponding extension of the fall season.

A secondary effect is the production of a sharp temperature inversion trapping moist air close to the water surface. Even in mid-summer very dense local fogs often hug the surface of the lake and adjacent rocky shores. These rarely extend inland, sometimes only enveloping the shore within 50 m or less of the lake (Fig. 20). On otherwise clear days, when the water–air temperature difference may reach as much as 7–8°C, small islets are frequently covered in a low fog layer. In 1973, on several occasions, we observed small islands completely covered in low fog layers, for example, the Leadman Islands (part of the Slate Islands), Hawk Island and the Macdonald Islands.

Direct observations on lake-shore microclimate were carried out at Cedar Bay near Thunder Bay

(Lindsay, 1968). The shore is subject to a land–sea breeze effect which develops nearly at right angles to the gradient westerlies and is most prevalent in June when 60% of the wind direction at nearby Lakehead airport is easterly. Temperatures taken along the rocky shore seldom exceed 15°C unless the wind shifted "offland" when it sharply increased by as much as 8.5°C. He suggested that high humidity and frequent fogs along the lake shore provide a blanketing effect for outgoing radiation resulting in a prolongation of the frost-free period in late summer and a corresponding slow warming in spring.

High heat loads are often experienced in open alpine environments at high elevations and in arctic regions. Cedar Bay measurements of incoming and outgoing solar radiation from rock surfaces showed that the total heat load on both surfaces of a plant leaf probably reach at least 2.25 g $cal/min^{-1}/cm^{-2}$ around noon on a sunny day. Of this, incoming sky radiation contributes only 0.46, the remainder being made up of rock surface radiation and reflection. The sky radiation figure is comparable with those for arctic and alpine environments; Webber (1974) cited representative values of 0.30 for Point Barrow in Alaska and 0.56 for Niwat Ridge in the Colorado Front Ranges. The high rock surface radiation figure was ascribed by Lindsay (1968) to the low albedo of dark surfaces characteristic of diabase and basaltic flows at Lake Superior. Thermal conductivity is also markedly high, particularly in comparison with values reported for limestones, granites and other rocks. Thus the effects of solar radiation are almost instantaneous with rapid heat conduction into crevices and a corresponding rapid heat loss. Effects such as this will be highly variable over short distances and may account, in part, for the extreme heterogeneity of assemblages of arctic-alpine plants at the lakeshore. In sites such as those described, trees and most shrubs are at a disadvantage compared with arctic-alpine herbaceous plants and sprawling subshrubs which are capable of surviving the stresses of life in a rock herbfield.

Canyon and Cliff Microclimate

A peculiar combination of circumstances allows the survival of arctic-alpine communities along the floors of canyons cut through diabase southeast of Lake Nipigon (Anonymous, 1973). Despite considerable searching of likely sites, only two canyons have been found to have significant numbers of arctic-alpine species: Ouimet Canyon and the

Fig. 20. Fog resulting from mid-summer temperature inversion, Pic Island.

valley at the head of Cavern Lake, northeast of Innes Lake.

These canyons have vertical sides and are so narow that the talus slopes from the two facing cliffs meet in the middle above the floor of the gorge (Fig. 10). Measurements at one site, calculated from map and abney level gave an estimated width of 100 m from rim to rim, a height of 30 m from the top of opposing talus slopes to the rim and a total depth of 60 m for the canyon. This is probably representative both for proportional and absolute measurements, although greater depths are mentioned for Ouimet Canyon.

During winter a considerable volume of ice is built up beneath and between the blocks of rock and its melting in spring and summer is inhibited by the protection given by overlying talus and by the north–south alignment of the gorge, which limits the time of exposure to full sunlight during the day. Close to the areas of ice accumulation in the canyons, arctic-alpine plants thrive at the edge of, or under, open-canopied boreal forest. *Pyrola grandiflora* and *Arenaria humifusa* are restricted to sites at Cavern Lake Canyon within a few metres of the ice (Table 6). Other species of wider tolerance occur nearby: *Dryopteris fragrans*, *Lycopodium selago*, *Polygonum viviparum*, *Saxifraga aizoon*, and *Woodsia glabella*.

Similar canyons may exist elsewhere, especially in the diabase sill area. An examination of aerial photographs has revealed sites worth investigating in the region west of Lake Nipigon. Soper and Maycock (1963) commented on the occurrence of ice about 2 m thick in a narrow chasm at Old Woman Bay in late June (June 23, 1961) and Agassiz (1850) noted persistent snow in a chasm in the same area in July of 1848.

Cliffs provide similar, though less extreme, habitats suitable for a range of arctic-alpine plants. Most are not stable and although crevices are colonized by opportunist herbs and shrubs, growth of trees is severely limited. South-facing cliffs provide extremes of temperature and tend to be colonized by species such as *Dryopteris fragrans* and *Saxifraga aizoon*. Cooler north-facing cliffs with shorter effective growing seasons provide habitats for species of *Woodsia*.

Direct effects of snow and ice

Although much of the rocky shoreline of Lake Superior has a thin cover of snow for long periods during the winter and early spring, there are heavy snowfalls in some areas. On the Canadian shore, long-term records indicate that the total winter snowfalls vary from 109 cm at Thunder Bay to 442 cm at Helen Mine, near Michipicoten and on the south shore in Michigan, similar snowfalls are usual, with Houghton-Calumet, on the Keweenaw Peninsula, having a long-term average of 465 cm. Thick snow accumulation is undoubtedly restricted by wind to crevices and ledges at some sites, actual depth of winter snow being indicated by the form assumed by stunted boreal forest trees such as *Abies balsamea* and *Picea glauca*. These sometimes occur as scattered individuals in shore herbfield, assuming a cushion "krumholz" form with low branches spreading more or less horizontally and any vertical stems pinched off and severely pruned of lateral branches (Fig. 21). The considerable periods of summer shoreline fog with a shortened growing season probably prevent adequate hardening of stems which are frosted and killed off if above the surface of winter snow; this has been suggested for similar growth forms in "krumholz" at the extreme upper limit of *Picea engelmannii* forest (Wardle, 1974). It greatly favours arctic-alpine vegetation lacking in erect shrubs and trees, with compacted life-forms and buds protected for winter.

Thrusting of ice sheets, detached from floes at the margin of the lake, may play a part in maintaining a herbaceous vegetation along much of the lakeshore. Local observations (Claude E. Garton, pers. comm. 1973) and winter photographs show

Table 6. Mid-summer temperature gradients in canyon at Cavern Lake.

Temp. (°C)	Distance from residual ice (m)	Position	Vegetation and phenology
2.5	2	Lee of talus block	No vascular vegetation
5.5	1	Sloping side of block	*Pyrola grandiflora* in leaf
16	2.4	Top of talus block	Same species flowering
24	16	Open talus slope in sun	No *Pyrola* present; vegetation that of normal sunny scree

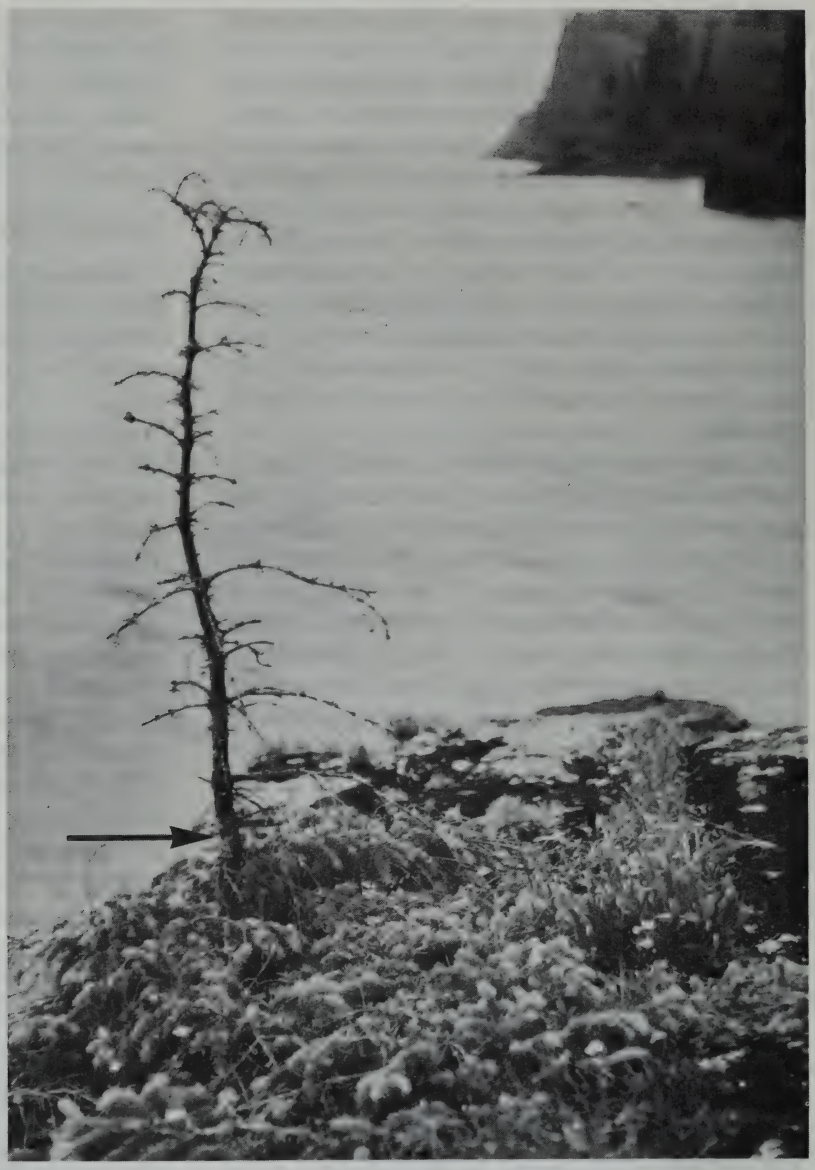

Fig. 21. Stunted *Abies balsamea* at exposed shoreline site on east side of Moss Island (Site no. 29). (The arrow marks probable maximum height of winter snow pack.)

that during storms sheets of ice are forced inshore and up onto land. At many sites along the north shore glacially smoothed rocks dip gently into the lake, particularly on the exposed outer coasts of peninsulas and islands between Rossport and Sibley Peninsula. Thrusting of ice onto the shore (commonly called "ice-push") will sheer off any tall vegetation unless well protected by crevices. At Lasher Island, damage to shrub vegetation exposed above the tops of crevices on shore platforms indicated that this mechanism has played a part in discouraging taller vegetation from developing along these shores.

Rocks and soils

Geological factors have been suggested as influencing distribution of plant species within the arctic. Thorsteinsson (1958) has suggested that on Cornwallis Island plant cover is related in the main to elevation above sea-level, effectiveness of solifluction, and type of bedrock although the relative effect is considered difficult to evaluate. With respect to the last factor, he notes that calcareous shale, argillaceous limestone, shale and clay seem to form soil suitable for plant growth whereas relatively pure limestone and dolomite do

not. In particular, the occurrence of Intrepid Bay outcrops can be correlated with plant cover. Thornsteinsson observes that a general view of the Arctic Archipelago bears out more fully the important influence of rock type on plant cover. In accounting for the "monotonous" floristic character of Melville Bugt in northwestern Greenland, Sorenson (1943) pointed out that the islands and coastlands there consist almost exclusively of non-calcareous formations, mainly gneiss and, more locally, granite, syenite and other acid rocks. To the north and south, at Cape York and on Umanap Island are sedimentary rocks, which are often rich in calcium carbonate. These localities are all noted as having a considerably richer flora that Melville Bugt. Holmen (1957) noted several species, including *Woodsia glabella*, as being found almost exclusively on basalt and dolomite in Peary Land. In the eastern Arctic, *Cerastium alpinum*, *Anemone parviflora* and *Braya humilis* are restricted to calcareous sites (Porsild, 1964). In contrast, acidic sites are preferred by *Empetrum*.

These observations apply generally, also, to the Precambrian Shield region of Canada. Apart from a group of ubiquitous species which do not appear to demonstrate preferences for particular types of soil or rock, most arctic-alpines are more abundant on sites underlain by sedimentary rocks, diabase and basalt, especially where rocks contain significant amounts of calcium (although they may not necessarily be calcareous in a petrological sense).

Of the 48 arctic-alpine species accepted by us as occurring at Lake Superior, 60% are reported as having throughout most of their range a definite preference for soils derived from calcareous rocks; of these, *Primula mistassinica*, *Saxifraga aizoon*, *Woodsia alpina* and *W. glabella* are generally regarded as being virtually restricted to strongly calcareous sites (Polunin, 1940; Porsild, 1955, 1964; Hultén, 1962, 1970). Information is incomplete for twelve species but some of these, e.g. *Elymus mollis*, *Festuca brachyphylla* and *Saxifraga cernua*, probably show no particular preference for rock type. Only seven species at Lake Superior (ca. 15%) tend to occur on soils derived from granite rocks: *Carex supina*, *Dryopteris fragrans* (also reported from calcareous sites at Gaspé by Scoggan, 1950), *Empetrum nigrum*, *Lycopodium selago*, *Rubus chamaemorus*, *Vaccinium uliginosum* and *V. vitis-idaea*. Of these the *Carex* and *Rubus* are notably restricted in distribution, occurring at only a few sites northwest of Lake Superior.

Distribution maps and site checklists indicate that the richest arctic-alpine assemblages at Lake Superior occur on Keweenawan diabase, basalt, and related rocks; Animikie slate, carbonates and associated volcanics; and locally on Keewatin sedimentary rocks, breccia and lava (Fig. 22). Syenite, trachyte and nordmarkite of the Coldwell Complex (see Pye, 1969, p. 76 *et seq.*), and gabbro and diorite of the Moss Harbour area on Black Bay Peninsula support communities containing fewer arctic-alpines. The poorest representation of arctic-alpine plants is found on early Precambrian acidic igneous and metamorphic rocks. On shores of diabase or basalt up to one-third of a herbfield stand may be arctic-alpine in affinity. At Old Woman Bay, south of Michipicoten, Soper and Maycock (1963) listed thirteen arctic-alpine species for "rock-barren tundra" containing a total of 40 species. The rocks at the site are described as "hornblende mica schist" and contrast with granites and other acidic rocks along most of the adjacent shoreline. Searching by Soper and others, north and south of Old Woman Bay, has shown that arctic-alpine plants are almost totally absent from numerous apparently suitable sites such as Agawa Bay and Montreal River. North of Old Woman Bay the bulge of Pukaskwa National Park extends into Lake Superior, its granite shores only interrupted near the Pukaskwa River where rocks similar to those at Old Woman Bay reach the shore. Surveys of representative sites along the shore have revealed few arctic-alpine plants (Anonymous, 1974). A surprising record is *Saxifraga aizoon* from Pointe la Canadienne, because the species is generally regarded as an obligate calciphile. However, the site is very close to the mapped boundary between granites and related rock types, sedimentary rocks, and mafic volcanics. Along the north shore between Pukaskwa and Nipigon there is greater variety in the type of exposed rock. At some localities such as Terrace Bay, basement rock is covered with beds of gravel. This variety is reflected in the greater variety of arctic-alpine species, including some such as *Primula mistassinica* and *Saxifraga aizoon* which elsewhere seem to show a preference for sites overlying rocks with significant amounts of calcium.

At shoreline sites there is generally a close relationship between soils and the underlying rock. Soil development is meagre. Rarely are structured

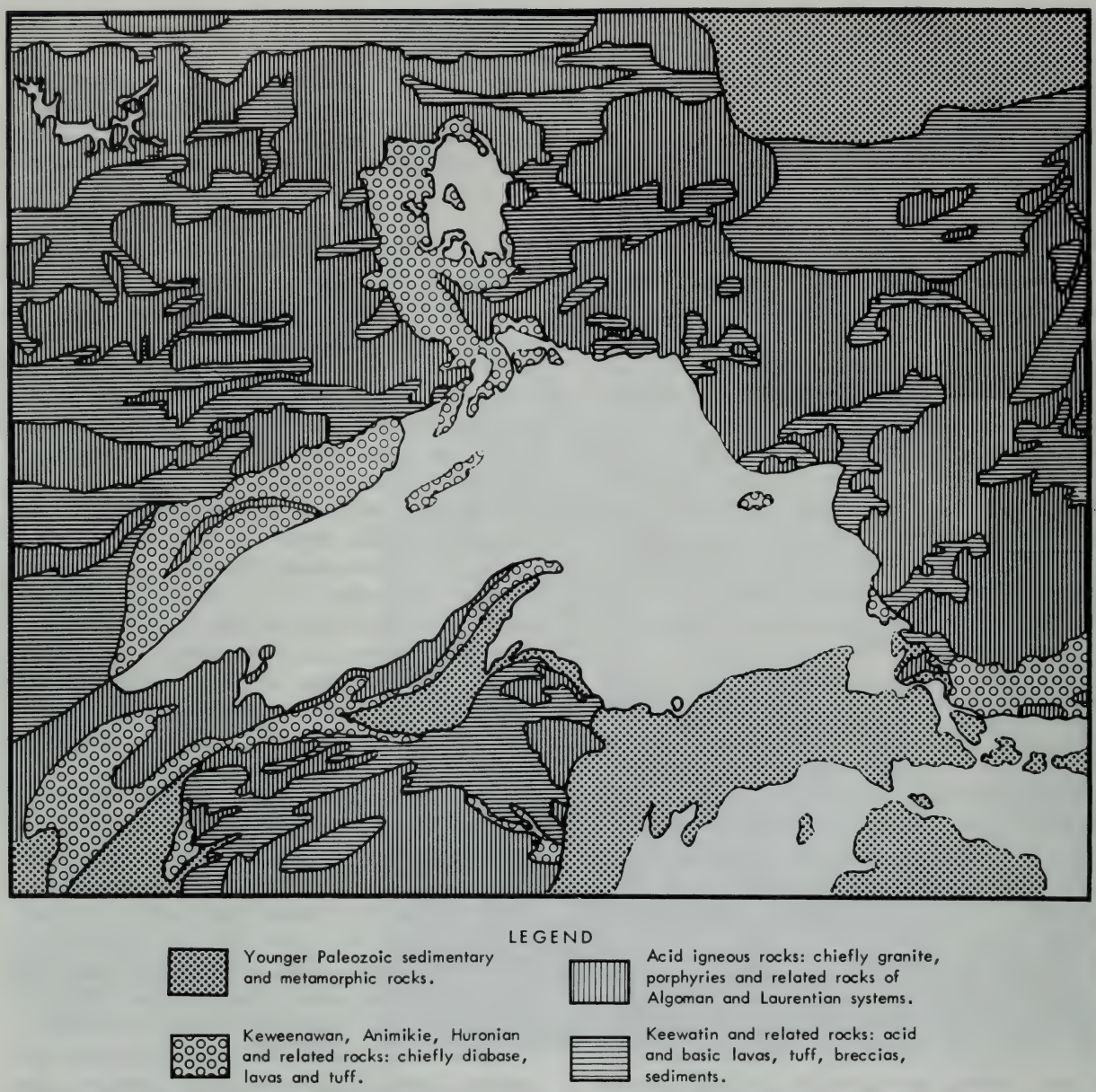
LEGEND
Younger Paleozoic sedimentary and metamorphic rocks.
Acid igneous rocks: chiefly granite, porphyries and related rocks of Algoman and Laurentian systems.
Keweenawan, Animikie, Huronian and related rocks: chiefly diabase, lavas and tuff.
Keewatin and related rocks: acid and basic lavas, tuff, breccias, sediments.

Fig. 22. Basement geology at Lake Superior. (Based on maps of the Geological Compilation Series, Ont. Dept. of Mines, 4 sheets covering Lake Superior, and on Geological Map of Canada, Geol. Surv. Can. Map No. 1250A. 1969)

profiles seen and usually soil of rocky shores consists of a mixture of fragments derived from the underlying rock and dark fibrous humus. Also, the soil is, for the most part, confined to crevices and ledges so that plant roots are in intimate contact with rock. Only around rock pools, in shallow swales and occasionally on cobble beaches are deeper, structured soils seen. On cliffs and talus slopes, plants are in close contact with solid rock and soil development is extremely limited.

A few of the species we have studied grow without being in direct contact with the underlying rock. *Elymus mollis* is confined to sandy, usually beach, sites. *Arenaria humifusa* grows in moss mats and *Rubus chamaemorus* in sphagnum hummocks. The failure of such species to migrate into areas apparently suitable but currently unoccupied is probably a result mainly of the effectiveness of intervening rocky shores and shallow soils as barriers to dispersal.

The physical nature of each rock type and its resistance to erosion and weathering play a part in determining which arctic-alpine plants will be supported. Diabase and basalt both weather into large

angular blocks, the size and shape of which are chiefly determined by the spacing and direction of joints and lines of weakness. As blocks are prised off a steep-sided outcrop, many ledges and depressions are formed. Fallen blocks break into angular pieces to form talus and the gradually enlarging cracks on the solid outcrop provide havens for numerous herbaceous species. Water percolating through fissures in basalt and diabase forms numerous seepages and, with wave splash, fills and replenishes rock pools. In contrast, granitic rocks and those of the Coldwell Complex, are more massive and less permeable. They lack definite fissures. Rather than being physically eroded they weather slowly to form smooth, relatively featureless surfaces. Lava flows and some dykes, especially where coarsely porphyritic, erode to give more or less rounded fragments in a gritty matrix. Where phenocrysts are conspicuous, a rough and knobbly surface results and provides a miniature nursery for many herbaceous plants.

Relatively soft and easily eroded rocks are not a favoured substrate for most arctic-alpine plants. In contrast to the north shore, many of the outcrops along the south shore of the lake are of softer sedimentary rocks. However, some arctic-alpine species do occur both at the northern end of the Keweenaw Peninsula where Keweenawan conglomerates outcrop and at Pictured Rocks on indurated sandstones (Wells & Thompson, 1974; Read, 1975).

Soil moisture

Fernald (1935) suggested that aridity and calcareous soils were limiting factors in the distribution of some arctic-alpines rather than coolness of climate. Damman (1965) has disputed this, pointing out that those species whose restriction is to the northwest of the Great Northern Peninsula of Newfoundland are also species of wet sites. At Lake Superior, few sites (except sand dunes and exposed cliff faces) can really be classed as xeric although Hosie (1938) referred to a "xerosere" along the shore at Batchawana Bay. Those species occurring away from the lake shore tend to occupy wet habitats such as cliffs (e.g. *Woodsia* spp.) or bogs (e.g., *Salix myrtillifolia*). Such sites are probably comparable to numerous subarctic or low-arctic habitats.

Competition

Competition is often believed to restrict arctic species to northern latitudes but, as already suggested, it is probably confined as a direct factor to interplant competition in interstices, crevices, ledges and rock-pool margins. Elsewhere the limiting determinants are stress and disturbance. Where competition is likely to play a major role is away from arctic-alpine communities. Arctic-alpine species are unlikely to compete successfully in boreal forest communities where, for much of the growing season, light levels are low near the ground.

DISTRIBUTION OF GROUPS OF SPECIES

Earlier, species were grouped according to their coincident distribution patterns at Lake Superior.

(a) Widespread species (Group A)

Members of this group are those which have broad ecological amplitudes and are able to persist, if not flourish, in several different community types. Group A contains all species recorded from three or more habitat types except *Saxifraga aizoon* (7 communities), *Empetrum nigrum* (5), *Sagina nodosa* (4) and *Vaccinium vitis-idaea* (4). They are frequent throughout the arctic where they similarly occupy a wide range of habitats. Two species of Group A are restricted to few communities. *Woodsia glabella* is known only from damp cliffs but its relatively wide distribution at Lake Superior is a reflection of the frequent occurrence of the habitat. *Scirpus cespitosus* is recorded only from splashpool communities but within these is ubiquitous.

In his studies of the Newfoundland flora, Damman (1965, 1976) has pointed out that the more widespread arctic-alpine species have a distribution pattern which appears to correspond to that of areas with low summer temperature regimes as measured by the sucrose inversion method. He noted that Dahl (1951) had observed that high summer temperatures are detrimental to arctic-alpine plants growing in cultivation. Damman concluded that intolerance for high temperature

explained the occurrence of many arctic-alpine species in closed plant communities far south of their usual range. The Newfoundland data suggest that, for arctic-alpine species which are relatively successful performers in southern outliers, average summer temperatures (T_e values) of 58°F (ca. 15°C) are critical. Almost all known localities for many species lie within areas with T_e values below this.

The species of Group A are, in general, successful performers at low latitudes particularly in the upper Great Lakes and the Gaspé-Nova Scotia region. Four out of eight arctic-alpine species found in northern Ontario and three out of six recorded by Hartley (1966) for the Driftless Area are from this group.

Even these species of Group A are not widespread in areas underlain by acidic rocks. At Lake Superior most are restricted to sites adjacent to the lake shore and are most abundant on diabase, basalt and sedimentary rocks. *Primula mistassinica* and *Pinguicula vulgaris* are virtually restricted to calcareous sites.

(b) Eastern species (Group B)

For *Sagina nodosa*, *Castilleja septentrionalis*, *Saxifraga aizoon* and *Elymus mollis* an eastern bias in their Lake Superior distribution is understandable in terms of their predominantly eastern pattern of distribution in North America. Outside the Lake Superior basin they are mid-arctic to low-arctic species extending south of the tundra at several places, especially along the shores of the Atlantic south to Cape Cod. *Elymus mollis* is a coastal species extending inland only to the shores of large lakes. Its pattern of distribution suggests late-glacial migration through the St. Lawrence Valley and the Great Lakes region but its eastern bias in the Lake Superior region is probably related directly to the distribution of sand dunes and beaches.

These species are generally less polymorphic and less successful colonizers than those of the previous group and in the Arctic are plants of shores and barrens occurring in well established communities. The single exception is *Sagina nodosa*, which can spread vegetatively and is a successful adventive in some areas outside its natural range. Damman (1976) suggested that *Carex scirpoidea* and *Saxifraga aizoon* have distribution patterns in Newfoundland which indicate that they are limited not only by summer temperatures but also by competition. Along with several other arctic-alpine species, they occur in colder parts of Newfoundland and on unstable basic or calcareous lowland sites. Although there is a general preference for the species of Group B to grow on calcareous sites, *Carex capillaris* and *C. scirpoidea* are only marginally calciphilous and *Empetrum* has a strong preference for acidic sites. These three species sometimes achieve on granite and related rocks an abundance which is not exhibited in other arctic-alpine species.

(c) Western species (Group C)

All are predominantly low-arctic shore or lake-edge plants, *Woodsia* extending its range of habitats to include damp, rocky cliffs and *Vaccinium* also occurring in wet shrubland. None is found in a wide range of communities and they are not prominent colonizers. South of the arctic they are confined to damp sites with an assured supply of moisture. Possibly they may be better regarded as boreal species, which, under mesic conditions, are capable of competing with other species in arctic, especially low-arctic vegetation.

(d) Species centered on the north shore (Group D)

These are not noted as pioneer species. In Newfoundland, with a large number of other species, *Tofieldia pusilla* is rather frequent throughout, although distinctly more common at higher elevations (Damman, 1965). *Vaccinium uliginosum* was regarded by Damman as typical of those species having their distribution determined by the summer temperature regime with T_e values below 58°F. (ca. 15°C). One feature of these species is that they are only weakly calciphilic and are able to tolerate acid soil conditions. This allows them to occupy sites which are not easily colonized by most other arctic-alpine plants. However, they do not appear to be highly successful in strong competition with more widespread species and are not widespread shoreline members of the arctic-alpine element.

(e) Restricted species (Pigeon River - Pic River) (Group E)

The most restricted plants in this group are mid-arctic to high-arctic in general distribution and in these zones they often play a pioneer role, which suggests that they may not compete successfully

with more aggressive plants at lower latitudes. *Saxifraga cernua* and *Dryas integrifolia* are ubiquitous in the arctic with wide ecological amplitudes (Polunin 1940; Porsild 1948, 1955). *Calamagrostis stricta*, *C. purpurascens*, *Hedysarum alpinum* and *Potentilla multifida* are mid-arctic to low-arctic and the first three are moderately good performers in enclaves in low latitude boreal zones. Damman (1965) suggested that such species may not be restricted in distribution by summer temperatures alone. He grouped *Cerastium alpinum* and *Pyrola grandiflora* with plants occurring at sites with particularly severe winter conditions, together with such species as *Carex bicolor*, *Cystopteris montana* and *Saxifraga cespitosa*. These tend to be moderately strong calciphiles and are virtually absent from areas underlain by acidic rocks. On the other hand, *Anemone parviflora* and *Dryas integrifolia* are grouped by Damman with those species occurring in Newfoundland in colder parts of the island and in unstable lowland sites, mostly on basic or calcareous rocks. Damman concludes that restricted species are eliminated from more favourable sites primarily be competition with other plants. This does not appear to apply strictly at Lake Superior; most of the species of this group appear to be at their extreme limits or range and will only occupy those habitats which present near-optimum conditions in terms of climate, soil type, and other factors. *Salix myrtillifolia* is found in low-arctic and subarctic sites from Alaska to Hudson Bay with a few stations further east (Dorn 1975). It occurs along streams and in poorly drained bogs.

(f) Other restricted species (Group F)

The final group presents a miscellany of plants including some about which we know very little. In general, these species are absent from the northernmost parts of Canada and from the eastern coastline although all except *Tanacetum huronense* are reported from the prairies. With the exception of *Festuca brachyphylla* and *Stellaria longipes*, all are most frequent in the Low Arctic and Subarctic. *Phleum alpinum* is a snowbed species and belongs to a segment of the arctic-alpine element which is virtually absent from the region. Damman (1976) grouped it with other common arctic plants such as *Cassiope hypnoides*, *Oxyria digyna*, *Phyllodoce coerulea* and *Sibbaldia procumbens* which are adpated to short growing seasons and require winter protection. Only in the canyons near Lake Nipigon and Thunder Bay might one expect to find some of these species, as yet unrecorded from Lake Superior. Lack of mountains in the Lake Superior basin and the exposed nature of the shorelines virtually preclude the development of significant protective snowbeds lying until late spring. For *Tanacetum huronense* and *Carex saxatilis* substrate is an important factor. These two are known only from sandy or rocky areas in the southeastern part of the Lake Superior area and in the Arctic they are predominantly shore plants.

ORIGINS OF THE ARCTIC-ALPINE ELEMENT

Glacial History

For cordilleran plants, including some arctic-alpine species found in northern Michigan, Fernald (1935) proposed the "nunatak" hypothesis, according to which part of the pre-Wisconsinan flora survived on ice-free land during continental glaciation. An explanation proposed earlier by Fernald (1925) and taken up some later authors (e.g., Calder & Savile, 1959) was that many such plants migrated post-glacially into the area from arctic and subarctic regions to the north, and from refugia such as the Driftless Area in southwest Wisconsin and adjacent parts of Illinois, Iowa and Minnesota. A third hypothesis (Butters & Abbe, 1953; Soper & Maycock, 1963) is that of survival in favourable habitats as relicts of a more continuous post-glacial distribution along the margin of continental ice. There is substantial evidence for a band of apparently discontinuous tundra-like terrain south of the Laurentide ice sheet, occupied by arctic-adapted plants and animals (e.g., Wright, 1971; Birks, 1976; Wayne, 1967).

Fernald's "nunatak" hypothesis has been largely abandoned in the face of evidence that the Lake Superior region was completely covered with ice prior to 12,000 years B.P. Erosion surfaces on ridge crests and bluffs as well as sheets of angular debris were interpreted by Fernald as indicating an

absence of glacial action. Later workers have found no evidence to suggest that the highest points in the Lake Superior basin were not overriden by Wisconsinan ice (Bergquist, 1937; Deevey, 1949; Richards, 1952a, 1952b; Prest, 1969, 1970). It seems more likely that aggregates of arctic-alpine plants at Lake Superior are relicts of more widespread distributions with a secondary role being played by migration.

Deglaciation of the Lake Superior Basin.—Details of the history of deglaciation and summaries of the complex late-Wisconinan lake system in the Superior basin have been given by several authors (Hough, 1958; Terasmae, 1967; Farrand, 1960, 1969; Wright & Watts, 1969; Prest, 1970; Wright, 1971, Saarnisto, 1974, 1975: especially Figure 17). The following summary is based on a study of these references.

About 12,800 years B.P., ice receded northwards from the western arm of the Superior basin. By 12,000 years B.P. the ice margin lay across the north end of the Keweenaw Peninsula, Isle Royale and Thunder Bay and was fronted by Glacial Lake Keweenaw. During the subsequent Valders Advance, ice again filled the whole basin but it receded rapidly so that by a little after 11,500 years B.P. the southwestern end of the basin was filled by an expanding proglacial lake (Lake Duluth). Ice recession was slow and a post-Duluth lake was formed that varied in size during a period of oscillating recession and advance between 11,000 and 10,000 years B.P. High-level, post-Main Algonquin lakes during this period extended from the Huron and Michigan basins into the southeastern Superior basin. Toward the end of these lake stages, the receding ice-margin extended along the line of the Dog Lake moraine to the present shore of Lake Superior near the Sibley Peninsula, southward to cut across Isle Royale and the northern tip of the Keweenaw Peninsula, striking the present Michigan shoreline near Pictured Rocks and followed this shore eastward as far as Whitefish Point. From here the ice front cut across the Lake Superior basin to reach the Canadian shoreline at Alona Bay between Mamainse Point and Montreal River; from Pictured Rocks to the Canadian shore it followed the line of the Cartier Morainic Belt. The rapid recession of the ice margin to the north shore of Lake Superior at about 9,500 years B.P. initiated the Lake Minong stage, during which most of the basin was flooded to a higher level than at present, the water level being controlled by a morainic threshold at Sault Ste. Marie (Saarnisto, 1975). At this time there was a steady and rapid fall in water level in the Superior basin and by 9,000 years B.P. the ice had receded north of the Lake Superior-Hudson Bay divide. Between this divide and the present position of Lake Superior, the Nipigon basin was occupied by Lake Kelvin and the Long Lac region was flooded to form Lake Nakina. Both lakes were bounded on the north by the receding ice front. If Glacial Lake Barlow-Ojibway drained into the Superior basin from the northeast as suggested by Prest (1970), this must have happened after 9,000 years B.P., perhaps via the headwaters of the Pic River (Saarnisto, 1975). During the Post-Minong stages, water levels fell rapidly to reach a low-water stage about 8,000 years B.P. when the Sault Ste. Marie threshold was eroded to bed-rock. Lake shorelines were lowered at a faster rate along the north shore of the lake system by differential isostatic uplift.

About 7,000 years B.P. rising water levels in the Huron and Michigan basins drowned the Sault Ste. Marie threshold and raised water levels in the Superior Basin, as part of the Nipissing transgression. Water levels reached a maximum about 5,000 years B.P. Since then, the shoreline of Lake Superior south of the Sault Ste. Marie isobase has been slowly submerging, whereas emergence of the coast north of this has continued.

Post-glacial Vegetation.—The hiatus in ice recession between 11,000 and 10,100 years B.P. described by Saarnisto (1974) as the Algonquin Interstadial, is characterized in the fossil record by a zone of non-arboreal pollen (NAP-zone). This zone has been recorded throughout much of northeastern Minnesota and western Ontario and along the eastern shores of Lake Superior. That period would have provided an environment particularly favourable to herbaceous plants adapted to cool climates with large areas of "raw" soil providing open habitats for opportunist tundra herbs. Proglacial lakes had open shoreline habitats washed by very cold water which might be ice-covered for much of the year. The freshly exposed habitats would have been marked by instability, as are sites of glacial recession today. Both proglacial lakes fed by glacial meltwater and adjacent large ice-sheets would have induced local climates with low mean temperatures and cool

cloudy summers, particulary during the Algonquin Interstadial (Terasmae, 1973; Potzger & Friesner, 1939). After discussing various estimates of the northward limits of forest cover adjacent to Wisconsinan ice, Wayne (1967) concluded that in the east central United States vegetation within 75 to 100 km of the ice was dominated by "wooded tundra" with white spruce in the taiga zone (Ritchie, 1959; Löve, 1959) in Manitoba. This compares favourably with other estimates of the breadth of a tundra or a taiga-parkland zone varying from about 80 to 150 km in the eastern United States (Manley, 1955; Dillon, 1956; Martin, 1958). Not only would local climate have been modified by the mass of ice in the wasting continental sheet but katabatic winds off the ice would inhibit establishment of trees on otherwise favourable sites. On Baffin Island, katabatic winds have caused depression of summer air temperatures by as much as 4.7°C at a distance of 1.5 km from a glacier terminus and cold air drainage also results in a high frequency of evening isothermal or inversion conditions (for details see Rannie, 1977).

Evidence suggests that in northern Minnesota and the upper Great Lakes Region the Wisconsinan ice sheet was flanked by a relatively widespread vegetation characterized by tundra plants. The lowest part of the pollen sequence in northeastern Minnesota at Spider, Weber and Kotiranta Lakes, and in southern Minnesota at Norwood, includes a late-glacial NAP-zone. Species identified from the zone are *Dryas integrifolia*, *Salix herbacea*, *Carex capillaris*, *Vaccinium uliginosum*, *Rhododendron lapponicum*, *Juncus balticus*, *Tofieldia pusilla*, *Arctostaphylos uva-ursi*, *Myriophyllum exalbescens*, *Hippuris vulgaris* and *Carex aquatilis* (Baker, 1964, 1965). Some of these, in particular, *Dryas integrifolia*, have been found in Minnesota as macrofossil remains (Watts, 1967). The NAP-zone at Weber Lake has been used to typify the Compositae-Cyperaceae Assemblage lying immediately above the Wisconsinan drift (Cushing, 1967). Confirmation of this earlier work is found in the detailed studies of pollen and plant macrofossil stratigraphy at Wolfe Creek in central Minnesota (Birks, 1976). Between 20,500 and 13,000 years B.P. non-arboreal vegeation dominated the region. Numerous macrofossil fragments have been recovered and NAP accounts for 60% or more of total pollen. Species identified include *Astragalus alpinus*, *Cerastium alpinum*, *Dryas integrifolia*, *Dryopteris fragrans*, *Sagina nodosa*, *Saxifraga tricuspidata* and *Vaccinium uliginosum* (all known at the present time from the Lake Superior basin), and *Armeria labradorica*, *Oxyria digyna*, *Rhododendron lapponicum*, *Saxifraga rivularis* and *Silene acaulis* (occurring south of the Arctic and other sites). *Shepherdia canadensis* *Athyrium filix-femina* and *Salix* spp. are often found in association with arctic-alpine disjuncts at Lake Superior.

Study of plant remains from a Cary-Port Huron interstade deposit near the northern tip of the Southern Peninsula of Michigan show that between 13,300 and 12,500 years B.P. this area supported tundra-like communities within the tundra-boreal forest ecotone (Miller & Benninghoff, 1969). Plants of arctic affinity recorded as macrofossils are *Bryum cryophilum*, *Carex supina*, *Dryas integrifolia*, *Salix herbacea* and *Vaccinium uliginosum* var. *alpinum*. The other identified macrofossils are chiefly boreal species extending into the Low Arctic. The occurrence of *Dryas integrifolia* is of particular interest as the continuous range of this species now lies well north of both the Upper Peninsula of Michigan and the Lake Superior basin. Miller and Benninghoff (in Plate 3 of their paper) map late-glacial fossil occurrences of this species from Minnesota and Massachusetts. In a description of late-glacial plants and plant communities in Northwestern New York, Miller (1973) drew attention to the occurrence of several fossil mosses near Lockport about 12,000 years B.P. These mosses are now known only from boreal and arctic regions. Two in particular, *Aulacomnium acuminatum* and *A. turgidum* indicate that tundra vegetation occurred there at that time. However, all fossil vascular plant remains at the site represent boreal forest rather than tundra species. Miller suggested that the mosses may have survived in micro-habitats along the strand of Lake Iroquois in sites similar to those found today along the margins of Lake Superior. *A. acuminatum* is currently known from the Arctic and a disjunct station at Ouimet Canyon, near the north shore of Lake Superior.

To the southeast, but from stratigraphically comparable sites, *Dryas integrifolia*, *Vaccinium uliginosum* and *Salix herbacea* have been found at Cambridge, Massachusetts (Argus & Davis, 1962); *Rhododendron lapponicum*, *Salix uva-ursi*, *Oxyria digyna*, *Arctostaphylos alpina* and *A. uva-ursi* in Hampshire County, Massachusetts (Emer-

son, 1898, cited in Argus & Davis, 1962); and *Salix reticulata* at Watkins Glen, New York State (Williams, Tarr & Kindle, 1909, cited in Hollick, 1931). At Colebrook, New Hampshire, an extensive deposit of fossiliferous lake sediments originally studied by Hollick (1931) has recently been reexamined by Miller and Thompson (1979). Among the macrofossils they have identified the following arctic-alpine species: *Selaginella selaginoides*, *Salix* cf. *uva-ursi*, *Oxyria digyna*, *Silene acaulis* var. *exscapa*, *Saxifraga aizoides*, *Sibbaldia procumbens*, *Dryas integrifolia*, and *Vaccinium uliginosum* var. *alpinum*. Accompanying these were fragments of numerous boreal species, including *Shepherdia canadensis*, *Arctostaphylos uva-ursi* and *Woodsia ilvensis*, which commonly occur along the Lake Superior shore at the present time. Other members of this assemblage represent species that exhibit the west-east North American disjunct pattern. These are *Salix vestita*, *Parnassia* cf. *kotzebuei*, *Dryas drummondii* and *Elaeagnus commutata*. They suggest that the occurrence of these at the site supports Rousseau's hypothesis that, as Quaternary glaciers receded, an "arctic corridor" adjacent to the ice-sheet provided suitable conditions for eastward migration of species (Rousseau, 1953). However, Miller and Thompson (1979) warned that although there is some evidence from the fossil record which may be consistent with this, and edaphic and climatic conditions may have allowed rapid, late-glacial migration, the fossil record is too incomplete to allow details of migration to be worked out.

On Long Island and eastern Staten Island near the extreme limit of Wisconsinan glaciation, reconstruction of the ice-margin vegetation at different times from 13,000 to 7,000 years B.P. (Sirkin, 1967) indicates the persistence of an NAP-zone at a time when the ice-margin was relatively static.

It is difficult to envisage the exact nature of the late Wisconinan ice-margin vegetation in this region. There may have been a zone of varying width approximating the present day taiga, rather than a simple barren-ground or rock tundra. Ritchie (1966, p. 76) summed up the difficulties when commenting that "it is unlikely that any vegetation exists today on a regional scale which is similar to the late glacial communities. One suspects that the late glacial spruce-dominated communites were youthful and primeval . . ." The heterogeneous list of plants known to be in the NAP-zone suggests a rather larger total flora than the late-glacial record has yielded. Ritchie suggested that a persistent search for further sites of sediments rich in macro-fossils will result in a growing list of late-glacial plants.

In a tentative reconstruction of the vegetation of the NAP-zone at Wolfe Creek, Birks (1976) proposed a mosaic of vegetation types with their differentiation being a function of slope, exposure and soil moisture. This would account for both the diversity and relative abundance of species recorded in the lowest parts of the Wolfe Creek sequence and would match ecologically, if not floristically, present-day sites in Alaska (Viereck, 1970), northeastern Saskatchewan (Argus, 1966), and northern Manitoba (Ritchie, 1959). Among the species now known from the lowest NAP-zone at Wolfe Creek are several pioneers. *Dryas* may have been exceedingly abundant as a colonizer of freshly exposed surfaces. Other pioneer species of glacial outwash gravels found at Wolfe Creek include *Arenaria rubella*, *Hedysarum* spp., and *Astragalus alpinus*. The last two genera (and *Dryas*) are known nodulating nitrogen fixers and would have been important agents in improving the soil. Pollen and plant macro-fossils near Colebrook (Miller & Thompson, 1979) indicate that, although the immediate landscape soon after ice recession (ca. 11,500 years B.P.) was predominantly treeless, a diverse flora was established. Absence of competition from trees and immaturity of the soil may have allowed heterogeneous associations to exist with nitrogen-fixing plants such as *Dryas*, *Shepherdia* and *Elaeagnus* in a pioneer role.

Inhibiting factors

Wright and Watts (1969) have shown that the tundra type vegetation which developed after ice recession was restricted to the northern part of Minnesota until as late as 10,000 years B.P. and was almost absent in the south. In interpreting this, Wright (1971) suggested that the history of ice-margin fluctuations is more complex than previously supposed. Adjacent lobes did not necessarily fluctuate synchronously and some advances (e.g., the Valders) may have resulted from glacial surges rather than from climatic change. He questioned the application of a simple climatic control for glacial advance and recession as well as assumed relationships of vegetation both to glacial

and to climatic changes. Generally, it seems reasonable to accept a fluctuating cool regional climate up to about 10,500 years B.P., then a sudden warming to give, by 8,000 years B.P., temperatures comparable to those existing at the present time (Terasmae, 1973). Temperatures warmer than at present prevailed to approximately 3,000 years B.P. Gradual cooling since then has led to temperatures which are probably like those of 9,000 years B.P., only a short time after the ice-sheet had left the Superior basin (Wright, 1969). Study of mastodon extinction rates in eastern North America (Dreimanis, 1968) supports the hypothesis of rapid climatic and vegetational change between 11,000 and 10,000 years B.P. Studies by Webb and Bryson (1972) and by Webb (1974) show a sequence of changes from colder and wetter to warmer and drier about 9,600 years B.P.

The rapid change in climate about 10,000 years B.P. seems to have been a critical factor in late-glacial revegetation of the north shore of Lake Superior. Terasmae (1967, 1968, 1973), Wright (1969) and Saarnisto (1974) have commented on the apparent absence of an NAP-zone immediately above Wisconsinan drift in northern Ontario. Terasmae (1973, p. 219) concluded that "by the time northern Ontario was deglaciated the climate had warmed sufficiently to allow mixing of arctic and boreal species in the vegetation that recolonised this region." There is little evidence for a late-glacial arctic flora near glacial Lake Barlow-Ojibway to the northeast of the Superior basin (Terasmae, 1963, cited in Terasmae, 1967); so Terasmae suggested that *either* boreal forest species colonized the better sites and crowded out less tolerant arctic species, *or* the arctic species may have migrated through the region rapidly. Terasmae's observations are supported by Saarnisto (1974) who found significant differences between the lowest parts of pollen profiles along the eastern shore of Lake Superior. Near Sault Ste. Marie the NAP-zone below the spruce-dominated zone is interpreted as indicating tundra vegetation with perhaps some trees being represented towards the top of the zone. The tundra-like phase lasted several hundred years after deglaciation before replacement by spruce forest. In contrast, pollen profiles from Alfies Lake (ca. 47° 53' N, 84° 51' W), a small lake 14 km south of Wawa, lack an NAP basal zone. Sedimentation at Alfies Lake started when the ice-margin was only about 10 km to the north and in the same horizon the lowest pollen zone, a spruce zone, already came to an end. Saarnisto interpreted this as indicating a colder climate following deglaciation at about 10,800 years B.P. in the Sault Ste. Marie region, compared with that in the Wawa area to the north.

We suggest that a powerful inhibiting factor in the successful recolonizing of tundra vegetation must have been the physical and chemical nature of the underlying hard-rock substrate. Contemporary distribution patterns of arctic-alpine plants indicate that most occur only sparingly on granitic rocks which produce acidic soils, being far more abundant on sedimentary, diabase or basalt substrates. Just as the arctic-alpine assemblages on granitic shorelines of Lake Superior are depauperate (e.g., along the Lake Superior shore of Pukaskwa National Park between Wawa and Marathon), so only impoverished floras would occupy similar sites along the receding ice-front. It is likely that, as the ice-front receded onto acidic rocks of the Canadian Shield between Sault Ste. Marie and Wawa, migration by non-arboreal tundra plants was slowed. Not only would impoverishment occur, but northward migration of tundra species would lag behind ice recession, allowing spruce and other species tolerant of acidic water-logged soil to catch up and supplant non-arboreal vegetation, after regional climate had ameliorated sufficiently to allow establishment of trees relatively close to the ice front. This should be detected in basal zones of pollen profiles from Pigeon River north to Lake Nipigon, across the boundary between Keweenawan diabase and Rove sediments and the older acid igneous rocks.

Once established, boreal forest north of Lake Superior has remained unchanged in its overall gross characteristics (Terasmae, 1967), although Terasmae later pointed out that isostatic rebound from glacial loading must have increasingly impeded the drainage. This, together with a change to cooler climatic conditions, has favoured the development of black spruce muskeg. W.K.W. Baldwin has termed this the "wet blanket" effect (cited in Terasmae, 1968; Baldwin, 1958) because in these regions the blanket of water and muskeg which is in evidence everywhere is a self-perpetuating system existing on a variety of substrates. When destroyed it rapidly regenerates forming a wet, acid barrier to migration of species not tolerant of such conditions. North of Lake Superior, wet blanket conditions have persisted to

the present time, providing an effective barrier in that region to the movement of most arctic-alpine tundra species and preventing migration with the retreating ice-front to reach and recolonise James Bay.

Formation of relict sites

Although speed of ice retreat was probably highly variable, it would not have been excessive for rapidly reproducing herbaceous and shrub species which would have been capable of colonizing and maintaining an intact non-arboreal zone immediately south of the retreating ice. Along the southern edge of this zone at an irregular interface with closed spruce forest there would have been gradual replacement by forest except at sites locally suited to a continuing tundra-like vegetation. Such sites approximated the cliffs, shores of lakes, and gorges where arctic-alpine plants persist today far south of their usual arctic and subarctic range. Some of these relicts, now separated from the main ice-margin tundra belt, must have disappeared when mean temperatures were significantly higher than at present. A feature of many of the Lake Superior shoreline sites is the great floristic diversity in small areas and it seems reasonable to assume that, along with survival of the species in favourable sites only, there was some concentrating of species from relatively large original areas into very much smaller refugia. The present arctic-alpine "tundra" communities at Lake Superior do not in a real sense represent unaltered persistent communities dating from the late-Wisconsinan (Soper and Maycock, 1963), but are better seen as concentrations from more widespread periglacial taiga and tundra, represented in the fossil record by the NAP zone immediately above Wisconsinan drift (Figure 23).

During the height of the Nipissing transgression, water levels were approximately 15 to 30 m higher than at present at Sault Ste. Marie and Michipicoten respectively (Saarnisto, 1975). At these and similar localities, arctic-alpine plants advanced to colonise rocky shores as they slowly emerged from the water. It can only be assumed that colonisation of islands was by dispersal from adjacent islands or mainland as soon as water levels had dropped sufficiently for the particular islands to emerge. The Slate Islands, for example, rise to a maximum altitude of 320 m at the west end of Mortimer Island. Extrapolation from Saarnisto's Figure (1975, Fig. 13) suggests that water levels would have dropped below this height at the Minong stage about 9,500 years B.P. when the ice margin lay just inland of the north shore of the lake. Propagules of pioneering species such as *Dryas integrifolia* would have had little difficulty bridging the 10 km gap between the shore and emerging Slate Islands, particularly under the influence of ice-generated katabatic winds. Within the Slate Island group, dispersal to some minor islets must have been relatively recent. The Leadman Islands lie about 3 km northeast of the main Slate Islands and are lower in maximum altitude; Leadman Island itself must have been submerged until about 3,000 years B.P. and Spar Island until 2,000 years B.P. although both carry well developed shoreline assemblages of arctic-alpine plants.

Migration routes

The changing pattern of spillways developed during deglaciation provided significant connecting links between adjacent basin systems and lowlands. Deep gorges which developed along disused spillways still provide refugia for arctic-alpine species stranded at these sites. *Rhododendron lapponicum* persists in Wisconsin (Wisconsin Dells and Kickapoo Valley) while the gorge of the Barron River in eastern Ontario harbours *Saxifraga aizoon* and *Dryopteris fragrans* (Brayshaw, 1964). Within the Superior basin, most major spillways which drained glacial Lake Agassiz have not been investigated for populations of stranded arctic plants although Ouimet and Cavern Lake Canyons may have been temporary spillways. To the north of these and west of Lake Nipigon, the Kaiashk spillway system opened as late as 9,500 years B.P. discharging via the Nipigon basin into the Superior basin. During late stages in deglaciation of the region this provided a good migration route for plants moving eastward into the area from the shoreline of Lake Agassiz which, by then, had transgressed to cover a vast part of southern Manitoba. Closure of the Kaiashk system for the last time almost coincided with the period of climatic change which saw an end to colonisation of ice-fee ground by tundra species.

Several arctic-alpine species at Lake Superior have distribution patterns suggesting a migratory connection with Lake Agassiz. *Vaccinium vitis-idaea*, *Senecio congestus*, *Euphrasia hudsoniana* and *Woodsia alpina* have predominantly western distributions within the Lake Superior basin.

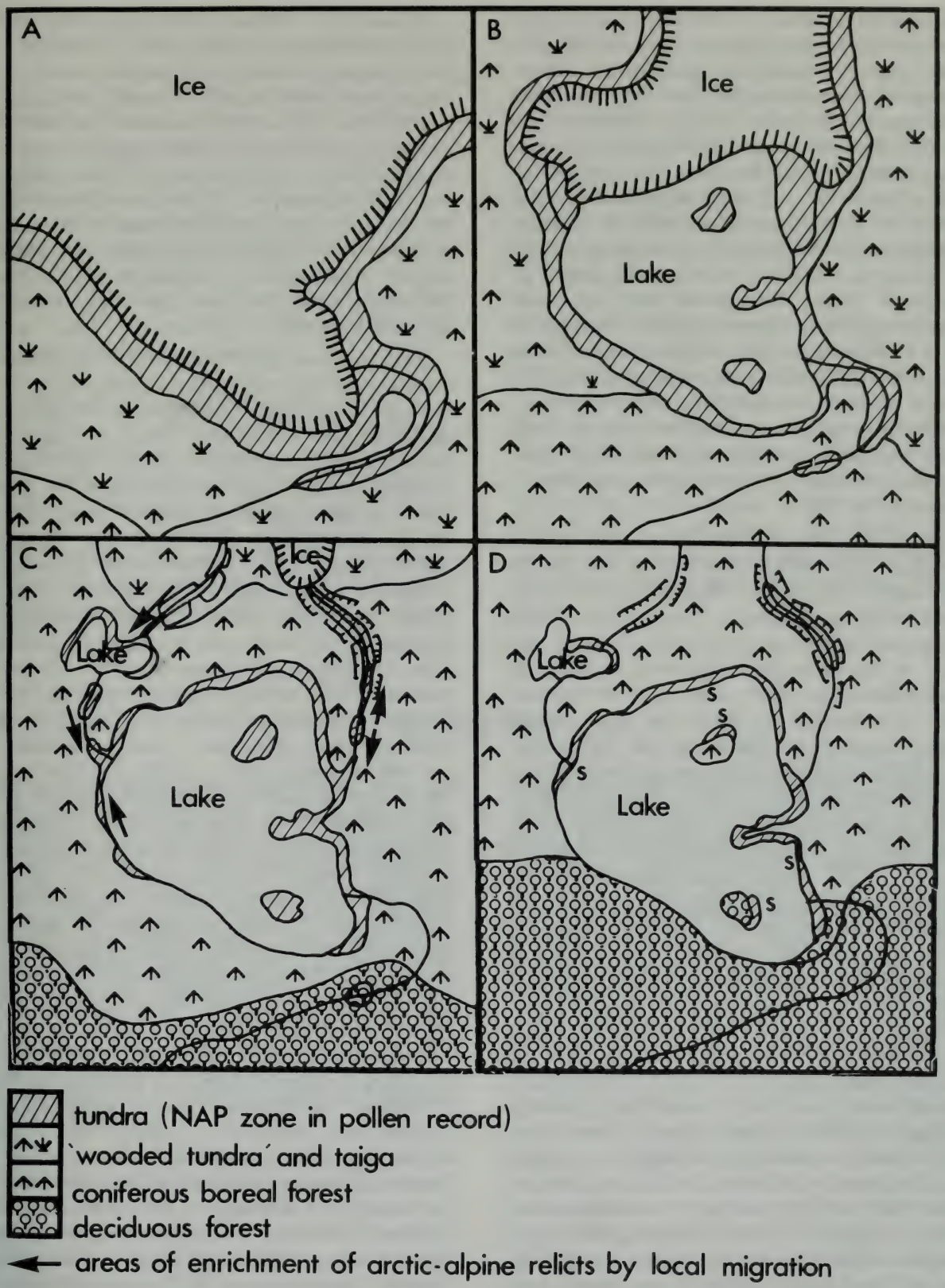

Fig. 23. Hypothetical stages in formation of relict sites with arctic-alpine species. A, full-glacial; B, early post-glacial; C, late post-glacial; D, present-day.

Euphrasia in its various forms is centred on Hudson Bay but extends into Manitoba and the area once occupied by Glacial Lake Agassiz. *Senecio congestus* occurs across the Low Arctic of North America but extends south to Labrador and through Manitoba, being known also from scattered sites at Lake Superior and in the Driftless Area. *Vaccinium vitis-idaea* and *Woodsia alpina* are rather more generally distributed although both have a marked gap in distribution from Lake Michigan and Lake Huron to the lower St. Lawrence Valley. Somewhat rarer at Lake Superior are *Carex supina*, *Saxifraga triscuspidata* and *Calamagrostis purpurascens*. The North American distribution of these is similar to that of *Senecio congestus*, southern extensions of range sweeping down through Manitoba and the basin once occupied by Lake Agassiz near Lake Superior. All are restricted to the northwestern sector of the lake.

Calder and Savile (1959) have suggested that *Saxifraga tricuspidata* survived in the Yukon–Mackenzie area of northwestern Canada during the Wisconsinan Glaciation. This area was ice-free throughout and there is increasing evidence that parts of the region and some areas flanking the Rocky Mountains to the south (e.g., the Nahanni and Liard Ranges) may have been major refugia during Wisconsinan Glaciation (see Vitt & Horton, 1979). Much of this region was blocked from areas farther south until about 12,200 years B.P., when a narrow corridor opened to the south. Assuming that migration might have commenced as soon as the corridor was open and that the latest date for arrival at the Superior basin would have been about 9,500 years B.P. (after which the Kaiashk spillway was closed and the development of tundra-like communities on deglaciated ground was inhibited), a minimum migration rate of approximately three kilometres every three years would have had to be maintained to cover the distance. Although the early part of the migration would have been over "raw" soils recently vacated by ice, as plants migrated south they would have encountered increasingly mature communities colonized from sites flanking the ice-sheet (Ritchie, 1976). Only if they could have occupied unstable sites or vacant niches would southeastward migration have continued. Significantly, *Saxifraga tricuspidata* has recently been found in the early post-glacial zones of Minnesota (Birks, 1976).

A significant spillway system may have been that connecting the Superior basin with those to the southeast. Transgression by the Champlain Sea as late as 9,800 years B.P. (see Hillaire-Marcel & Occhietti, 1977), provided a potential shoreline route for migration of coastal species, including several of arctic affinity, into the Michigan-Huron basin. From here, a route was available through the Bruce Peninsula and Manitoulin Island to the southeast end of the Superior basin. This route, mainly consisting of shoreline calcareous substrates, would have been particularly suitable for tundra species.

Eight species at Lake Superior have distribution patterns with an eastern bias within the basin, although found from Pigeon River to Pic River in numerous sites. Of these, *Empetrum nigrum*, *Carex capillaris* and *Carex scirpoidea* are unlikely to have migrated into the area from the east. *Carex capillaris* appears in the NAP-zone of the late glacial pollen record in northern Wisconsin and must have been a member of the ice-margin vegetation. *Carex scirpoidea* and *Empetrum* are closely associated species that are widespread through the Subarctic and Arctic at the present time. The remaining five species have distribution patterns which strongly suggest migration from the east. *Castilleja septentrionalis*, *Saxifraga aizoon* and *Sagina nodosa* are virtually restricted to an eastern coastal and low-arctic distribution in North America and are currently known from the lower part of the St. Lawrence Valley. *Saxifraga aizoon* requires a route over calcareous substrates and the Bruce Peninsula–Manitoulin Island pathway might have provided this. *Sagina*, being a shoreline plant, would be well fitted to migrate along the shore of the Champlain Sea and into the Upper Great Lakes. *Selaginella selaginoides* and *Elymus mollis* have rather wider distribution patterns in North America, but like *Sagina*, are often shoreline plants which would have no difficulty migrating from the St. Lawrence Valley during the Champlain transgression. Other species whose present day distribution patterns in North America indicate possible migration into the Superior basin from the east are *Draba norvegica*, *D. incana*, *Lycopodium alpinum*, *Phleum alpinum*, *Primula mistassinica*, *Dryopteris fragrans* and *Pinguicula vulgaris*. Obligate calciophiles such as the two species of *Draba* and *Primula mistassinica* would be particularly favoured by the Bruce Peninsula–Manitoulin Island route, where

open limestone habitats may have been maintained until a late stage of deglaciation. The predominantly eastern North American distribution of the *Draba* species, *Phleum alpinum* and *Tanacetum huronense* demand either an eastern origin or large-scale post-glacial reductions in range west of Lake Superior. *Tanacetum huronense* presents an interesting case. It occurs on shoreline sites in the Lake Superior region only at the southeastern corner of the lake. Its failure to colonise apparently suitable sites farther around the lake appears merely to be the result of local barriers to dispersal in the form of rocky granitic shores lacking beaches.

Although proglacial lakes in the Superior basin periodically drained through southern spillways, particularly in the earlier stages of deglaciation, it is unlikely that they functioned as important migration routes separate from the main ice-front migration of the tundra biota. There is no evidence that arctic species of tundra-like vegetation persisted in areas to the south of the Superior basin long enough to provide a significant source of arctic immigrants as the Lake Superior region underwent deglaciation. What northern plants remain in the Driftless Area today are almost all remnant populations of boreal rather than arctic species and the only disjunct arctic-alpine species currently shared with Lake Superior are *Primula mistassinica*, *Senecio congestus*, *Lycopodium selago* and *Dryopteris fragrans*. There is also little evidence to support the suggestion of Potter (1932) that marine introgression may have opened up a direct route from the St. Lawrence to James Bay through the Lake Abitibi region. Some colonisation of Hudson Bay may have taken place as ice retreated rapidly northwards after 9,000 years B.P. but it is likely to have involved only a few species suited to acid soils or gravel shorelines. This may account for scattered records of several arctic-alpine species (e.g., *Vaccinium uliginosum*, *Castilleja septentrionalis* and *Euphrasia hudsoniana*) in Northern Ontario. As at Lake Superior, populations of these species only persist where local microclimate and soils approximate those of the Arctic rather than the surrounding boreal regions.

SUMMARY

Arctic-alpine plants have been known from the Lake Superior region since the early part of the nineteenth century. Greatest concentrations occur along the shore of Lake Superior between the Pigeon and Pic Rivers, with secondary centres at Lake Nipigon, inland from Thunder Bay, the Border Lakes, Michipicoten Island, near Wawa and Keweenaw Peninsula. Forty-eight species are accepted as constituting the arctic-alpine element of the vascular flora. This includes taxa occurring in the Arctic but generally absent from boreal and prairie zones. Species are excluded where there is taxonomic doubt or where the geographic range is imperfectly known.

Assemblages of plants including arctic-alpine species are classified and the use of the terms "arctic-alpine" and "community" in the description of these is justified. Use is made of numerical techniques in grouping relevés, computational strategies being REMUL, Maximal Predictive Classification (MPC) and DIVINF. Thirteen communities are recognised. These are grouped into five classes, the most widespread of which are rock herbfield and rock-pool herbfield. Performance of arctic-alpine species within communities is assessed. Only 16% occur in five communities or more (*Trisetum spicatum* in 8; *Poa glauca*, *Polygonum viviparum*, *Primula mistassinica* and *Saxifraga aizoon* in 6; *Empetrum nigrum* and *Pinguicula vulgaris* in 5). Just over 30% play a definitive role in a particular community but many of the species are minor constituents. Widespread arctic-alpine species at Lake Superior tend to be those with known wide ecological amplitudes.

The geographic ranges of all arctic-alpine species at Lake Superior were studied, both within this region and throughout North America. The majority reach their greatest abundance in subarctic or mid-arctic zones. Other regions where arctic-alpine plants occur south of the Arctic are discussed. That most similar to Lake Superior is the Gulf of St. Lawrence; 42 of the species found at Lake Superior occur there. Only a few of the arctic-alpine plants found in the study area are recorded

from the Driftless Area southwest of Lake Superior. Within the Lake Superior basin the arctic-alpine species are arranged into six groups on the basis of distribution pattern: widely distributed (9 species), having an eastern bias (8 species), frequent between Pigeon River and Pic River (3 species), having a western bias (4 species), uncommon and restricted to Pigeon River – Pic River (17 species), and a residue of 7 uncommon species whose distributions do not match any of the others.

Chief factors proposed as maintaining arctic-alpine habitats in the area are stress and (to a lesser degree) disturbance. Shoreline microclimate is probably a major factor in association with direct effects of snow and ice, rock and soil types and minor contributions from competition and soil moisture. An important feature of Lake Superior is the maintenance of low water temperatures throughout the year. The peculiar combination of circumstances allowing survival of arctic-alpine species in canyons south of Lake Nipigon is described.

Known history of deglaciation and post-glacial vegetation and our studies of contemporary occurrences of arctic-alpine plants at Lake Superior suggest that this region is a refugium originating from more widespread vegetation fronting the retreating Wisconsinan ice-sheet. Climatic change favouring boreal coniferous forest as well as acidic granitic-derived soils have effectively stopped colonisation of northern Ontario by most arctic-alpine species. Some migration may have occurred via late-glacial spillways from Glacial Lake Agassiz and the Champlain Sea but this was probably of minor importance. Migration between Lake Superior and the southern part of Hudson Bay was probably insignificant.

Two appendices are included: an annotated checklist of arctic-alpine species at Lake Superior and a list of sampling sites for vegetation analysis.

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Appendix A. ANNOTATED CHECKLIST OF ARCTIC-ALPINE VASCULAR PLANTS AT LAKE SUPERIOR

The 48 taxa which have been selected as constituting the arctic-alpine element of the vascular flora at Lake Superior are listed below in alphabetical order. Nomenclature for the most part follows standard floristic accounts of the North American Arctic except where recent revisions have altered the sense of older epithets or introduced new ones. Where, in several instances, there are differing taxonomic interpretations, a conservative approach has been adopted. Brief comments on nomenclature and taxonomy are included. Citation of specimens is restricted to a selection, including our own collections when available, rather than giving a complete listing of all material from the region in local herbaria. Under distribution, herbarium and publication records are included where the species is rare and local and the entry is preceded by an asterisk (*). Otherwise a generalized distribution only is given, firstly for Lake Superior and adjacent areas, then for the whole range. Where published distribution maps have been seen, this is indicated. Habitat comments are based on the scheme adopted in this paper with brief notes on arctic preferences.

**Anemone parviflora* Michx. (Ranunculaceae)

DISTRIBUTION: Slate Islands: north shore of Mortimer Island, 27 July 1937, Hosie *et al.* 1881 CAN; Mortimer, Patterson and DeLaute Islands, 1973, Soper & Given obs.; Leadman Islands: northeast corner of Leadman Island, 1 July 1973, Soper & Given 13110 CAN, CHR, MICH; same place, 23 June 1974, C.E. Garton 15915 CAN, LKHD, MICH. Aguasabon River, 26 July 1967, Soper & Dickinson 11905 CAN; Pic River area, 1883, J. Macoun (unconfirmed report). North American low-arctic - subarctic (mid-arctic). Map: Porsild (1964).

HABITAT: *Saxifraga-Arctostaphylos* and *Carex-Sagina* rock pool herbfield (B.1. and B.2.). In Arctic: sheltered heath, mossy stream banks, bird nesting sites, calcareous soils.

**Arenaria humifusa* Wahl. (Caryophyllaceae)

DISTRIBUTION: In the canyon northeast of Cavern Lake, 4 July 1972, C.E. Garton 15029 CAN (the first collection for the Lake Superior area); same place, 24 July 1972, C.E. Garton 15086 CAN, LKHD, MICH; same place, 10 July 1973, Soper & Given 13170 CAN, CHR, MICH. (Fig. 17) Amphi-Atlantic low-arctic (high-arctic - subarctic) - cordilleran. Maps: Hultén (1958), Porsild (1964).

HABITAT: *Pyrola* talus herbfield (E.1.). In Arctic: moist calcareous gravels, rock crevices, cryptogamic communities.

Sometimes included as a variety under *A. ciliata* L.; included are *A. longipedunculata* Hult. and *A. cylindrocarpa* Fern.

**Astragalus alpinus* L. (Fabiaceae)

DISTRIBUTION: Michipicoten Harbour, stream near Minto Mine, 24 Aug. 1938, Hosie *et al.* 1728 CAN, DAO; Sleeping Giant: east side, 8 July 1936, Taylor *et al.* 679 CAN, GH; crest, 14 July 1947, C.E. Garton 1038 DAO. Circumpolar mid-arctic - subarctic (high-arctic) -cordilleran. Maps: Hultén (1970), Porsild (1964).

HABITAT: Thin soil on basalt ledges. In Arctic: well-watered calcareous sandy and gravelly sites, grassy tundra, bird nesting sites, sometimes a pioneer.

Extremely variable with numerous infraspecific taxa described: Lake Superior plants are referable to ssp. *alpinus* (low-arctic diploid), sometimes segregated with plants from the lower St. Lawrence as var. *brunetianus* Fern.

**Calamagrostis purpurascens* R.Br. (Gramineae)

DISTRIBUTION: Sleeping Giant: crest, 12 July 1970, C.E. Garton CAN; top, 24 August 1956, C.E. Garton DAO. Talus Bay, Sibley Peninsula, 24 June 1936, T.M.C. Taylor *et al.* 1974 CAN. Mountain Lake, 7 July 1938, F.K. Butters *et al.* CAN. North American low-arctic - subarctic (mid-arctic) - cordilleran. Map: Dore & McNeill (1980), Porsild (1964).

HABITAT: Cliff (D.1.). In arctic: calcareous sandy or rocky places, xerophilous, probably characteristic of sites with little winter snow.

**Calamagrostis stricta* (Timm) Koeler (Gramineae)

DISTRIBUTION: South Bay at Lake Nipigon, 26 July 1960, C.E. Garton DAO; St. Ignace Island, south side, 18 August 1959, C.E. Garton DAO; Border Lakes area (Butters & Abbe, 1953); Keweenaw Peninsula and Kalamazoo County, Michigan (Voss, 1972). Circumpolar low-arctic - subarctic (mid-arctic) - cordilleran. Maps: Dore & McNeill (1980), Hultén (1962), Porsild (1964).

HABITAT: Sand beach and dune herbfield/grassland (C.2.). In Arctic: wet prairies, meadows, lake shores, sometimes a pioneer.

Long known under the name *C. neglecta* Gaertn., Mey. and Scherb. and frequently confused with *C. inexpansa* Gray.

***Carex capillaris* L.** (Cyperaceae)

DISTRIBUTION: Generally throughout the northern and eastern portions of the Lake Superior region from Thunder Bay to Batchawana Bay; Keweenaw Peninsula; also around the upper parts of Lake Michigan and Lake Huron. Circumpolar mid-arctic - subarctic - cordilleran. Maps: Hultén (1962), Porsild (1964).

HABITAT: *Saxifraga-Arctostaphylos* and *Carex-Sagina* rock pool herbfields (B.1. and B.2.). In Arctic: marshes, heaths, stream sides, sometimes preferring calcareous soils.

Highly variable; Lake Superior plants probably ssp. *chlorostachys* (Steven) Löve, Löve & Raymond, which is low-arctic - boreal; also known as var. *elongata* Fern. and var. *major* Blytt.

***Carex saxatilis* L.** (Cyperaceae)

DISTRIBUTION: Corbeil Point, east shore of Lake Superior, 20 July 1935, T.M.C. Taylor *et al.* 484 TRT: a single station disjunct from the nearest continuous areas around James Bay. (Fig. 18) Circumpolar - high arctic - subarctic - temperate. Maps: Hultén (1962, 1968), Porsild (1964).

HABITAT: Among rocks on beach; (not seen but probably A.3.). In Arctic: shallow water of tundra ponds, edges of small lakes, heath, fen, sedge marsh and intertidal mud or sand flats.

Our treatment includes *C. saxatilis* var. *miliaris* (Michx.) Bailey and var. *rhomalea* Fern.; the TYPE of *C. miliaris* Michx. is from the vicinity of Lake Mistassini, Quebec.

***Carex scirpoidea* Michx.** (Cyperaceae)

DISTRIBUTION: Scattered from Sibley Peninsula to Old Woman Bay; Lake Nipigon, Keweenaw Peninsula and Drummond Island, Michigan; also on the Bruce Peninsula and Manitoulin Island and on the shores in the upper part of Lake Huron and Georgian Bay. (Fig. 13B) Amphi-Atlantic - mid-arctic - subarctic - cordilleran. Maps: Hultén (1958), Porsild (1964).

HABITAT: *Potentilla-Sagina* rock herbfield (A.3.), *Carex-Sagina* rock pool herbfield (B.2.). In Arctic: dry turfy sites, stony barrens and hummocks, often with a preference for calcareous sites.

Treatment differs considerably between authorities and the infra-specific variation is considerable.

***Carex supina* Wahl.** (Cyperaceae)

DISTRIBUTION: Clearwater Lake in Border Lakes area (Butters & Abbe, 1953); South Fowl Lake (Bailey, 1892); North Fowl Lake, 14 July 1973, Morton & Venn CAN, WAT. Circumpolar low-arctic (mid-arctic - subarctic). Maps: Hultén (1962), Porsild (1964).

HABITAT: *Dryopteris-Woodsia* talus (E.2.). "on cliff talus where northfacing well drained slopes carried little vegetation" (Butters & Abbe, 1953, p. 131). In Arctic: non-calcareous dry rocky, gravelly and sandy sites; xerophytic.

North American plants belong to spp. *spaniocarpa* (Steud.) Hult. This species should be sought in nearby Ontario locations.

***Castilleja septentrionalis* Lindl.** (Schrophulariaceae)

DISTRIBUTION: Montreal River to Pigeon River along shore; Michipicoten Island; Isle Royale; Keweenaw Peninsula; Grand Portage (Butters & Abbe, 1953); (Figs. 4B, 13A). Eastern North American low-arctic (subarctic). Map: Porsild (1964).

HABITAT: Sand beach and dune herbfield/grassland (C.2.). In Arctic: damp rocky soils, outwash, sometimes preferring serpentine or calcareous soils.

***Cerastium alpinum* L.** (Caryophyllaceae)

DISTRIBUTION: North Fowl Lake (Butters & Abbe, 1953); Leadman Islands: Leadman Group, 30 July 1937, R.C. Hostie *et al.* 599 CAN; Leadman Island. 1 July 1973, Soper & Given 13107 CAN, MICH; Spar Islet, 23 June 1974, C.E. Garton 15913 CAN, LKHD, MICH; same place, 1 July 1973, Soper & Given 13097 CAN. (Figs. 2, 4A) Asian - North American high-arctic (mid-arctic - low-arctic) - cordilleran. Map: Porsild (1964).

HABITAT: *Potentilla-Sagina* rock herbfield (A.3.), *Saxifraga-Arctostaphylos* rock pool herbfield (B.1.). In Arctic: calcareous gravels and cliffs, snowbed gullies, calcareous talus.

We have included *C. beeringianum* Cham. & Schl. in our concept of this taxon, which Polunin (1940, p. 189) dismissed as "a sort of rubbish heap for certain specimens that I have not been able to understand." Porsild (1964) separated the two species and, on the basis of his characters, Lake Superior plants are nearer to *C. alpinum*, although some collectors have referred them to the other.

***Draba aurea* Vahl.** (Cruciferae)

DISTRIBUTION: Thunder Cape, Sleeping Giant and Middlebrun Bay (all on Sibley Peninsula - specimens at CAN). North America and Greenland low-arctic - subarctic - cordilleran. Map: Porsild (1964).

HABITAT: A shoreline species but no specific data. In Arctic: dry gravelly slopes and meadows.

***Draba incana* L.** (Cruciferae)

DISTRIBUTION: Islets at north end of Isle Royale (Gull Island, W.S. Cooper GH; Passage Island, Povah & Brown 3671B MICH; same place, 9 August 1975, E.G.

Voss 14716 GH, LKHD, MICH, MSC). Amphi-Atlantic low-arctic (subarctic): in North America from Churchill eastwards. Maps: Hultén (1958), Mulligan (1970).

HABITAT: A shoreline species found in rock crevices and on rock outcrops (D.1.). In Arctic: moist to dry turfy or bare sites; calcareous boulders and cliffs.

Variable with several indeterminate varieties described; Fernald regarded Lake Superior plants as var. *incana*. Brown (1937) noted the species under *D. arabisans* Michx. var. *orthocarpa* Fern. & Knowlt., but the specimen seen is neither this nor the similar *D. hirta* L.

**Draba norvegica* Gunn. (Cruciferae)

DISTRIBUTION: Susie Island near Pigeon River (south shore), 2 August 1937, Abbe & Abbe CAN, GH. Amphi-Atlantic low-arctic (mid-arctic - subarctic); in North America from eastern James Bay eastwards. Maps: Hultén (1958), Mulligan (1970).

HABITAT: Talus, "localized on a disintegrating dyke south shore of island off the southwest end of Susie Island" (annotation on the specimen cited). In Arctic: rocky ledges and cliffs.

**Dryas integrifolia* Vahl. (Rosaceae)

DISTRIBUTION: Thunder Bay District: Thunder Bay, Lake Superior, Hosie *et al.*, 1924 CAN - cited by Porsild (1948) refers to the following collection: Slate Islands, DeLaute Island, 31 July 1937, R.C. Hosie *et al.* 1924 CAN. Other collections from the Slate Islands include: DeLaute Island, 1 July 1973, Soper & Given 13076 CAN; Barnard Point (not Bernard Point as on some labels) on Mortimer Island, 30 June 1973, Given & Soper 73162 CAN, CHR, MICH; Mortimer Channel on Mortimer Island, 22 June 1974, C.E. Garton 15904 CHR, LKHD, MICH. North American high-arctic - subarctic (extreme arctic) - cordilleran. Maps: Miller & Benninghoff (1969), Porsild (1964).

HABITAT: *Carex-Sagina* rock pool herbfield (B.2.). In Arctic: ubiquitous pioneer on clay or gravel barrens, calcareous talus and cliffs, open sandy heath; marked by a very wide ecological amplitude.

Dryopteris fragrans (L.) Schott (Polypodiaceae)

DISTRIBUTION: Widespread along shore and inland from Duluth to Batchawana Bay; occasional in Porcupine Mountains, Huron Mountains and Keweenaw Peninsula on the south shore; North Channel of Lake Huron (Britton & Soper, 1966). Circumpolar mid-arctic - low-arctic (subarctic). Map: Hultén (1962).

HABITAT: *Potentilla-Sagina* rock herbfield (A.3.), *Saxifraga-Arctostaphylos* rock pool herbfield (B.1.), cliffs (D.1.) and *Dryopteris-Woodsia* talus (E.2.). In Arctic: cliffs, screes, open moraines, generally on non-calcareous soils.

North American plants are referable to var. *remotiuscula* Komarov.

Elymus mollis Trin. (Gramineae)

DISTRIBUTION: Northern and eastern sector of Lake Superior from Thunder Bay to Batchawana Bay; local from Chapel Beach to Whitefish Point, Michigan (Voss, 1972): Guire & Voss (1963). Circumpolar mid-arctic - low-arctic (subarctic) - littoral along western and eastern North American coasts. Maps: Dore & McNeill (1980), Hultén (1962).

HABITAT: Sand beach and dune herbfield/grassland (C.2.). In Arctic: sandy shores, dunes, gravel beaches.

Sometimes treated as an infraspecific category of *E. arenarius* L. (as ssp. *mollis* (Trin.) Hult., or var *villosus* Meyer) and some records in eastern North America may be based on that species (Guire & Voss, 1963). Segregated by some others as *Leymus mollis* (Trin.) Pilger.

Empetrum nigrum L. (Empetraceae)

DISTRIBUTION: Pigeon River along north shore to Montreal River; Pictured Rocks area in Alger County, Michigan (Read, 1975); Keweenaw Peninsula (Richards 2212A, MICH); Isle Royale; Michipicoten Island; Caribou Island: Soper & Voss (1964); shore of Lake Superior in Luce County, Michigan, 30 August 1974, E.G. Voss 14510 BLH, GH, LKHD, MICH, MSC, NY and Mackinac County, Michigan (E.G.Voss, pers. comm., 1980). Circumpolar mid-arctic - subarctic (high-arctic) - cordilleran. Maps: Hultén (1970), Porsild (1964).

HABITAT: *Saxifraga tricuspidata* rock herbfield (A.2.), *Empetrum* rock heath (A.4.), *Carex-Sagina* rock pool herbfield (B.2.). *Calamagrostis-Ledum* rock pool herbfield/shrubbery (B.3.), transitional herbfield/shrubbery (C.1.). In Arctic: heaths, bogs, dry heathy areas; usually restricted to acidic non-calcareous soils.

In the absence of agreement among different authors we have treated this species conservatively. Variation is chiefly in fruit colour and shape, leaf and stem pubescence and glandularity, and the monoecious versus dioecious state. Butters and Abbe (1953) recognized both *E. nigrum* and *E. hermaphroditum* Fern. & Wieg. at Lake Superior. In 1959, Löve and Löve applied the epithet *E. hermaphroditum* (Lange) Hag. to all North American plants. Some authors have reduced the latter to subspecific status under *E. eamesii* Fern. & Wieg. (Löve, 1960).

Euphrasia hudsoniana Fern. & Wieg. (Schrophulariaceae)

DISTRIBUTION: Duluth to Pic River; Isle Royale; also Christina Bay, Manitoulin Island, 28 July 1974, J.H. &

J.E. Soper 13392 CAN. (Fig. 15B) Eastern North American subarctic (low-arctic).

HABITAT: *Carex-Sagina* rock pool herbfield (B.2.), *Calamagrostis-Ledum* rock pool herbfield/shrubbery (B.3.). In Arctic: gravelly and rocky places especially shorelines, clearings.

In their revision of the North American species, Sell and Yeo (1970) pointed out that there has been considerable confusion in the use of this epithet and several others; Lake Superior records of *E. frigida* and of *E. "arctica"* should be referred here. They recognized three varieties, all of which occur at Lake Superior; these seem difficult to uphold in the field.

**Festuca brachyphylla* Schultes (Gramineae)

DISTRIBUTION: Michipicoten Island, 23 July 1971, C.E. Garton *et al.* CAN; Slate Island: François Island, 1 July 1973, Soper & Given 13070 CAN; southwest corner of Patterson Island, 1 August 1973, C.E. Garton 15531 CAN. LKHD, MICH; Black Bay Peninsula: islet between Black's Wharf and Lasher Island, 8 July 1973, Soper & Given 13140 CAN; possible records from Grand Marais (Butters & Abbe, 1953). Circumpolar extreme arctic - low-arctic (subarctic). Maps: Dore & McNeill (1980), Hultén (1962), Porsild (1964).

HABITAT: *Saxifraga tricuspidata* rock herbfield (A.2.), *Saxifraga-Arctostaphylos* rock pool herbfield (B.1.). In Arctic: ubiquitous in dwarfed vegetation with dry summer soils.

Sometimes included in *F. ovina* L., or regarded as a variety of it. At lower latitudes it approaches *F. saximontana* and some specimens labelled as *F. brachyphylla* should be referred to this species. Fernald (1935) noted the occurrence of *F. brachyphylla*-like plants at Keweenaw and Butters & Abbe (1953) discussed the occurrence of similar plants at Grand Marais where they grow in very exposed shoreline sites. They retained their plants in *F. saximontana*, a treatment adopted also by Dore and McNeill (1980). The Michipicoten collection of Garton contains three pieces referable to *F. saximontana* and one which seems to be *F. brachyphylla*.

**Hedysaryum alpinum* L. (Fabaceae)

DISTRIBUTION: East side of Lake Nipigon; near Rossport; Sibley Peninsula near Silver Islet; Black River, Aguasabon River; Gravel River; White River; shore of White Lake, 21 July 1972, E.G. Voss 14030 MICH. Circumpolar low-arctic (subarctic). Maps: Hultén (1970), Raup (1947).

HABITAT: Sandy lakeshore (C.1.) and cliffs near shoreline (D.1.). In Arctic: riverbanks, moist thickets and prairies, gravel bars and rocky slopes.

Porsild (1964) accepted this species for the lower Mackenzie River valley and western Arctic only. North American plants belong to ssp. *americanum* (Michx.) Hult.

**Lycopodium alpinum* L. (Lycopodiaceae)

DISTRIBUTION: Keweenaw Peninsula, 30 June 1895, O.A. Farwell 849 BLH, US. Circumpolar subarctic (low-arctic) - cordilleran; in North America markedly disjunct and absent from central boreal-arctic Canada. Map: Hultén (1958).

HABITAT: We lack sufficient evidence to allocate this to a community at Lake Superior. In Arctic: cliffs, rocky slopes.

Lycopodium selago L. (Lycopodiaceae)

DISTRIBUTION: North shore of Lake Superior from Duluth to Old Woman Bay, inland to Lake Nipigon; Isle Royale; Michipicoten Island; Keweenaw Peninsula (Billington, 1952); Cornucopia in Bayfield County, Wisconsin (Tryon *et al.*, 1953); several Michigan counties between Lake Superior and Lake Michigan (Hagenah, 1962). (Fig. 11B) Circumpolar - mid-arctic - subarctic (high-arctic) - cordillern. Maps: Hultén (1962), Porsild (1964).

HABITAT: Transitional herbfield/shrubbery (C.1.), cliffs (D.1.), *Dryopteris-Woodsia* talus herbfield/shrubbery (E.2.). In Arctic: wet peaty tundra, cold cliffs, heath, marshes, barren grounds, often seeming to avoid pure limestone.

Very variable and part of a complex of closely related species. Lake Superior plants have been placed in var. *selago* and var. *patens* (e.g., Butters & Abbe, 1953; Tryon *et al.*, 1953) but the distinctions seem slight in the field. This taxon is sometimes referred to the genus *Huperzia*.

**Phleum alpinum* L. (Gramineae)

DISTRIBUTION: Keweenaw Peninsula, O.A. Farwell (several collections) BLH, US; Pukaskwa (unconfirmed report cited in Anonymous, 1974). Circumpolar subarctic (low-arctic) - cordilleran; in North America generally eastern. Maps: Dore & McNeill (1980), Hultén (1958).

HABITAT: Shore rocks (no further information available). In Arctic: meadows, river ledges, stream banks, damp open slopes, often somewhat protected especially at higher elevations.

Some authors have placed North American plants in the species *P. commutatum* Gaud., but, in view of the need for a monographic treatment of the genus, we have adopted a conservative approach and retained Lake Superior specimens in *P. alpinum*.

Pinguicula vulgaris L. (Lentibulariaceae)

DISTRIBUTION: Whole north shore of Lake Superior; Keweenaw Peninsula, Marquette and Pictured Rocks on

the Michigan shore; also along shores in the upper parts of Lake Huron and Lake Michigan (Fig. 11A). Amphi-Atlantic but almost circumpolar low-arctic - subarctic - cordilleran. Maps: Hultén (1958), Porsild (1964).

HABITAT: *Potentilla-Sagina* rock herbfield (A.3.), all rock pool herbfield (B.1. - B.3.), cliff herbfield (D.1.). In Arctic: moist soils by streams, lakes, bogs, often in calcareous sites although sometimes tolerating acid soils.

**Poa alpina* L. (Gramineae)

DISTRIBUTION: Recorded from Lake Superior by Agassiz (1850), Cooper (1914) and Fernald (1935). Other records include the following collections: ONTARIO: Heron Bay, 19 July 1964, E.G. Voss MICH, TRT. MICHIGAN: Isle Royale, 1868, A.E. Foote, MICH; Blake Point, 1975, E.G. Voss 14764 LKHD, MICH; Keweenaw County, 1898, O.A. Farwell 1616C BLH, MICH; also known from northern Lake Huron: Christina Bay, 19 July 1959, Soper & Heidenreich 8869 CAN, TRT. A specimen collected on rocky shores, Lake Superior (locality not stated, but probably Otter Head) by John Macoun, 27 July 1869 CAN No. 35833, was labelled as this species but has been redetermined as possibly *P. nemoralis* by A.E. Porsild. Amphi-Atlantic low-arctic and subarctic - cordilleran. Maps: Dore & McNeill (1980), Hultén (1958), Porsild (1964).

HABITAT: Shoreline rocks (no further details). In Arctic: snowbeds, meadows, ridges, dry slopes, talus, most frequent in rich humus at edge of snowbeds, sometimes showing a preference for calcareous soils.

This species is a variable agglomerate of generally apomictic biotypes in which several infraspecific taxa have been described.

Poa glauca Vahl (Gramineae)

DISTRIBUTION: North shore from near Duluth to Batchawana Bay; Lake Nipigon; Longlac; Isle Royale; Keweenaw Peninsula; Marquette County, Michigan; also in northern part of Lake Michigan and of Lake Huron. Circumpolar mid-arctic - subarctic (high-arctic) - cordilleran. Maps: Dore & McNeill (1980), Hultén (1962), Porsild (1964).

HABITAT: *Potentilla-Sagina* rock herbfield (A.3.), rock pool herbfield (B.1. - B.3.), cliff herbfield (D.1.). In Arctic: widespread and often a pioneer, sometimes a calciophile.

Polunin (1940, p. 67) described this taxon as a "veritable typus polymorphus" agreeing with M.P. Porsild (1920, p. 41) that it "varies without limits according to the quality of the place." It grades into *P. nemoralis*, *P. arctica*, *P. alpina*, *P. laxa* and *P. pratensis*; for Lake Superior, Butters & Abbe (1953) recognized several infraspecific taxa. In their discussion of *Poa* adjacent to the lake, they noted the great variability both within and between populations (Butters & Abbe, 1947).

Polygonum viviparum L. (Polygonaceae)

DISTRIBUTION: Thunder Bay to Lake Superior Provincial Park, along shore; Livingstone Point, Lake Nipigon; Isle Royale; Michipicoten Island; Minnesota shore (where noted as rare), Butters & Abbe (1953); Pigeon Point, Belle Rose Island, Lucille Island, Grand Marais; Keweenaw Peninsula, W.S. Cooper GH. Circumpolar high-arctic - subarctic (extreme-arctic) - cordilleran. Maps: Hultén (1970), Porsild (1964), Soper (1963), Soper & Maycock (1963).

HABITAT: *Potentilla-Sagina* rock herbfield (A.3.), *Saxifraga-Arctostaphylos* rock pool herbfield (B.1.), *Carex-Sagina* rock pool herbfield (B.2.), transitional herbfield/shrubbery (C.1.). In Arctic: almost ubiquitous except in driest sites, preferring manured sites.

Sometimes referred to the genus *Bistorta*.

**Potentilla multifida* L. (Rosaceae)

DISTRIBUTION: Lake Nipigon, Mungo Park Point, 9 July 1884, J. Macoun CAN; Silver Islet, Sibley Peninsula, 19 July 1936, T.M.C. Taylor *et al.* 1328 CAN; same place, 15 August 1955, Löve & Löve 6915 CAN, WIN; same place, 27 July 1950, C.E. Garton 1218 DAO, GH, MICH. There is some doubt as to the identity of a Garton specimen collected 11 June 1970 CAN. Circumpolar subarctic. Map: Hultén (1970).

HABITAT: Rocky shores and dry stone ridges. In Arctic: rocky shores, dry sites, outcrops, gravel bars and scree slopes.

Primula mistassinica Michx. (Primulaceae)

DISTRIBUTION: North shore from Duluth to Sault Ste. Marie and inland to Lake Nipigon; near Longlac; White Lake area; Isle Royale; Michipicoten Island; Apostle Islands; Keweenaw Peninsula; Marquette County, Michigan; Pictured Rocks; also in the upper parts of Lakes Michigan and Huron. North American subarctic - temperate. Maps: Soper *et al.* (1965, 1972).

HABITAT: *Potentilla-Sagina* rock herbfield (A.3.), rock pool herbfield (B.1. - B.3.), transitional herbfield/shrubbery (C.1.), cliff herbfield (D.1.). In Arctic: limestone pavements and open meadows, cliff faces, river margins, ledges, rarely far from underlying calcareous rock.

Following recent treatments by Vogelmann (1960) and Soper *et al.* (1965, 1972) this taxon includes *P. intercedens* Fern. The species is virtually confined to calcareous soils.

**Pyrola grandiflora* Rad. (Ericaceae)

DISTRIBUTION: Ouimet Canyon and a canyon NW of Cavern Lake, northeast of Thunder Bay: Ouimet Canyon, 7 October 1969, C.E. Garton CAN; same place

1 July 1976, C.E. Garton 17071, MICH; canyon NW of Cavern Lake, 10 July 1973, Soper & Given 13167 CAN, MICH. (Fig. 17) Circumpolar mid-arctic and low-arctic (extreme-arctic - low-arctic). Maps: Hultén (1958), Porsild (1964).

HABITAT: *Pyrola* talus herbfield (E.1.). In Arctic: snow patches and lee of outcrops, dry tundra, possibly calciophilous.

This should be regarded as a subspecies of the European *P. rotundifolia* (*P. rotundifolia* L. ssp. *grandiflora* (Rad.) Andres) according to E. Haber (pers. comm., 1979).

Ranunculus lapponicus L. (Ranunculaceae)

DISTRIBUTION: Various sites both along the shore and inland through the Nipigon basin, from the Border Lakes to Pic River; 20 miles NE of Grand Marais, Minnesota (cited by Coulter & Fisher, 1893), which is probably the same locality as the record from "three miles west of Mawshequawcawmaw River" which Butters & Abbe (1953, p. 149) identified as the Reservation River; also known from Chippewa County, Michigan. (Fig. 16A) Circumpolar low-arctic - subarctic. Maps: Hultén (1970), Porsild (1964).

HABITAT: Bog herbfield/grassland/sedgeland (C.3.). In Arctic: bogs, muskegs, often under willows.

Sagina nodosa (L.) Fenzl (Caryophyllaceae)

DISTRIBUTION: North shore from Pigeon River to Batchawana Bay; Isle Royale; Keweenaw Peninsula; Michipicoten Island. Amphi-Atlantic (almost circumpolar) low-arctic (subarctic). Maps: Crow (1978), Hultén (1958), Porsild (1964), Soper (1963), Soper & Maycock (1963).

HABITAT: *Arabis-Sagina* rock herbfield (A.1.), *Potentilla-Sagina* rock herbfield (A.3.), *Saxifraga-Arctostaphylos* rock pool herbfield (B.1.), *Carex-Sagina* rock pool herbfield (B.2.). In Arctic: margins of ponds, salt marshes and shores, moist peaty or silty soils.

Sometimes referred to the genus *Spergula*. Crow (1978) referred Lake Superior specimens to *Sagina nodosa* ssp. *borealis* Crow which occurs in the subarctic of North America, along the Gulf of St. Lawrence – New England coast, and at Lake Superior.

**Salix myrtillifolia* Anderss. (Salicaceae)

DISTRIBUTION: 11 miles east of Longlac 29 July 1952, Baldwin & Breitung 3573 CAN (cited in Dorn, 1975); canyon NW of Cavern Lake, 10 July 1973, Soper & Given 13171 CAN, MICH; Pukaskwa, 12 July 1977, C.E. Garton 17778 CAN, LKHD, MICH; Black River, 1 km NW of Rouse Lake, 8 July 1977, C.E. Garton 17763 CAN, LKHD, MICH. North American subarctic. Maps: Dorn (1975), Soper & Heimburger (in press).

HABITAT: bog herbfield/grassland/sedgeland (C.3.). In Arctic: bog and muskeg, especially along streams.

Specimens from the canyon NW of Cavern Lake and from 11 miles east of Longlac (at Lukinto Lake) are not var. *cordata* (Anderss.) Dorn, but other Lake Superior collections have been determined as that variety by G.W. Argus (see Dorn, 1975).

Saxifraga aizoon Jacq. (Saxifragaceae)

DISTRIBUTION: Border Lakes along shoreline and from several inland sites to Old Woman Bay; Lake Nipigon; Isle Royale; Michipicoten Island; Keweenaw Peninsula; Gros Cap; also reported from the Bruce Peninsula (Shivas *et al.*, 1969) and from Algonquin Park (Reznicek *fide* E.G. Voss, pers. comm., 1980). Amphi-Atlantic low-arctic (mid-arctic - subarctic). Maps: Hultén (1958), Porsild (1964), Soper (1963), Soper & Maycock (1963).

HABITAT: *Saxifraga-Arctostaphylos* rock pool herbfield (B.1.) *Carex-Sagina* rock pool herbfield (B.2.), transitional herbfield/shrubbery (C.1.), cliffs (D.1.), talus herbfield (E.1. and E.2.). In Arctic: apparently limited to calcareous sites, rocks, gravel.

North American plants are often differentiated as variety *neogaea* Butters.

**Saxifraga cernua* L. (Saxifragaceae)

DISTRIBUTION: Mountain Lake in Border Lakes region, east end, 5 July 1937, F.K. Butters *et al.* GH. Butters and Abbe (1953) noted two collections from this site. Circumpolar extreme arctic - low-arctic (subarctic) - cordilleran. Maps: Porsild (1964), Hultén (1970).

HABITAT: Upper margin of fine talus; *Dryopteris-Woodsia* talus herbfield/shrubbery (E.2.). In Arctic: a wide range and apparently indifferent to snow cover, drainage and exposure.

**Saxifraga tricuspidata* Rottb. (Saxifragaceae)

DISTRIBUTION: Islets flanking Black Bay Peninsula from Tunnel Island to Hawk Island. ONTARIO: Marcil Bay, 8 July 1973, Soper & Given 13164 CAN; Perley Island, 9 July 1973, Given & Soper 73287 CAN; Tunnel Island, 9 July 1973, Given & Soper 73298 CAN; Hawk Island, 5 July 1973, Given & Soper 73244 CAN. MICHIGAN: Isle Royale: Scoville Point, 1 July 1930, C.A. Brown MICH; North Government Island, 19 July 1974, E.G. Voss 14488 LKHD, MICH and other recent collections by E.G. Voss at MICH. (Fig. 17) North American high-arctic - subarctic - cordilleran. Maps: Calder & Savile (1959), Porsild (1964).

HABITAT: *Saxifraga tricuspidata* rock herbfield (A.2.), *Saxifraga-Arctostaphylos* rock pool herbfield (B.1.), cliff herbfield (D.1.). In Arctic: ubiquitous, often abundant on poorly covered dry slopes and accumulating aeolian grit.

Calder and Savile (1959) placed the Lake Superior

plant from Isle Royale (the only specimen from the region examined by them) in forma *tricuspidata*.

Scirpus cespitosus L. (Cyperaceae)

DISTRIBUTION: Widespread along the lakeshore from Duluth to near Batchawana Bay, inland to Lake Nipigon; Isle Royale; Michipicoten Island; Caribou Island; Keweenaw Peninsula; Voss (1972) noted it from Marquette, Alger and Chippewa Counties, also the upper parts of Lakes Michigan and Huron. (Fig. 12). Probably circumpolar low-arctic - subarctic - cordilleran. Map: Porsild (1964).

HABITAT: *Potentilla-Sagina* rock herbfield (A.3.), rock pool herbfield (B.1. - B.3.). In Arctic: moist depressions, sedge meadows, sedge heath tundra, bogs, barrens and river gravels.

Selaginella selaginoides (L.) Link (Selaginellaceae)

DISTRIBUTION: Scattered stations along lake shore from Grand Marais to Batchawana Bay; inland to Lake Nipigon, White Lake and near Wawa; Isle Royale; Eagle Harbor on Keweenaw Peninsula, 13 July 1936, F.J. Hermann 7994 GH; northwest of Hurley, Wisconsin (Tryon *et al.*, 1953); also inland in several locations in Michigan (Voss, pers. comm., 1980); in the upper part of watershed of Lake Michigan, Lake Huron and Georgian Bay. (Fig. 14) Discontinuous circumpolar subarctic (low-arctic) - cordilleran. Maps: Hultén (1958), Porsild (1966).

HABITAT: *Saxifraga-Arctostaphylos* rock pool herbfield (B.1.); also in cedar swamps, inland (C.3.). In Arctic: moist ledges, gravels, swamps and meadows.

**Senecio congestus* (R.Br.) D.C. (Compositae)

DISTRIBUTION: Recorded from a few Minnesota stations (Lakela, 1965); near the Pigeon River and at Lake Nipigon; Whitefish Lake, C.E. Garton, LKHD. We have omitted from the map a record of a collection (in ALBC) made in 1934 by C.H. Swift from just south of the Straits of Mackinac in Emmet County, Michigan, which has remained unconfirmed. This species is considered as "probably extinct" in Michigan by Wagner *et al.* (1977, p. 106). (Fig. 15A) Circumpolar high-arctic - mid-arctic (low-arctic - subarctic). Maps: Hultén (1970), Porsild (1964).

HABITAT: Bog herbfield/grassland/sedgeland (C.3.). In Arctic: commonly moist sites near the sea; marshes, tarn margins.

There is strong morphological and geographical evidence that two taxa are included in this species although separation into variety *congestus* and variety *palustris* (L.) Fern. (the former arctic and the latter low-arctic to boreal) is not successful in resolving this possible combination of elements. Hirtellous rather than strongly villous plants, including those at Lake Superior, have been referred to variety *tonsus* Fern., but this separation appears to lack taxonomic significance.

**Tanacetum huronense* Nutt. (Compositae)

DISTRIBUTION: The Lake Superior localities for this species are concentrated at the eastern end of the lake and the species is commonly found all along the Michigan shore from Whitefish Point to Grand Sable; also along and near the shores of James Bay and Hudson Bay. ONTARIO: Harmony River, 16 Sept. 1935, T.M.C. Taylor *et al.* 1599 CAN; Havilland Bay, 1935, Pease & Ogden GH. MICHIGAN: Vermillion, east of Whitefish Point, 1961, E.G. Voss 9929 GH, MICH, TRT. On the Agassiz expedition of 1848, a collection was made (but labelled simply "Lake Superior") by C.G. Loring GH; also known from the shores of the upper parts of Lake Michigan and Lake Huron (west side). North American (part of circumpolar complex) subarctic - low-arctic. Maps: Guire & Voss (1963), Hultén (1970).

HABITAT: Sand beach and dune herbfield/grassland (C.2.) In Arctic: chiefly on riverbanks and beaches out of direct influence of salt spray.

Sometimes merged with the related *T. bipinnatum* Sch. Bip. at the subspecific level; both species are referred to *Chrysanthemum* in some floras, e.g., Hultén (1968), the taxon treated above then becoming *Chrysanthemum bipinnatum* L. ssp. *huronense* (Nutt.) Hultén. Fernald recognized several races of *Tanacetum huronense*.

**Taraxacum ceratophorum* (Ledeb.) DC. (Compositae)

DISTRIBUTION: Spar Island, 1 July 1973, Soper & Given 13084 CAN, MICH; Patterson Island, 3 July 1973, Given & Soper 73212 CAN; Mortimer Island, C.E. Garton 15907 LKHD, MICH; Leadman Island, C.E. Garton LKHD. North American (low-arctic) - subarctic - cordilleran. Map: Raup (1947).

HABITAT: Transitional herbfield/shrubbery (C.1.). In Arctic: grassy places often near sea beaches.

Tofieldia pusilla (Michx.) Pers. (Liliaceae)

DISTRIBUTION: Scattered along shore from Sibley Peninsula to Oiseau Bay, Pukaskwa; Isle Royale and islets (Voss, 1972); Grand Marais and Two Harbors in northeastern Minnesota (Butters & Abbe, 1953). (Fig. 16B) Circumpolar low-arctic - subarctic - cordilleran. Maps: Hultén (1962), Porsild (1964).

HABITAT: *Carex-Sagina* rock pool herbfield (B.2.). *Calamagrostis-Ledum* rock pool herbfield/shrubbery (B.3.) In Arctic: moist turfy sites, wet moss, marshes, moist depressions in heath, dry rocky barrens, hillock tundra and frost polygons.

Occasionally incorrectly placed in synonymy with *T. palustris* Huds.

Trisetum spicatum (L.) Richt. (Gramineae)

DISTRIBUTION: Common along the north shore of Lake Superior and on islands from Duluth to Gros Cap near Sault Ste. Marie, inland to Lake Nipigon; Keweenaw Peninsula; Isle Royale; Michipicoten Island; Pictured Rocks, Alger County (Read, 1975) and Marquette County, Michigan (Voss, 1972); also on Drummond Island, Lake Huron and on Beaver Island, Lake Michigan. Circumpolar high-arctic - low-arctic (subarctic) - cordilleran. Maps: Hultén (1962), Porsild (1964), Soper & Maycock (1963).

HABITAT: *Saxifraga tricuspidata* rock herbfield (A.2.), *Potentilla-Sagina* rock herbfield (A.3.), rock pool herbfield (B.1. - B.3.), transitional herbfield/shrubbery (C.1.), cliff herbfield (D.1.), *Dryopteris-Woodsia* talus herbfield/shrubbery (E.2.). In Arctic: dry sandy ridges, herbmats, damp depressions, rocky sites, fellfield, often a good indicator of late snow lie.

The conclusion of Hitchcock *et al.* (1969, p. 723) that, "well-marked geographic races are not delimitable although several workers have evidently felt that they were," probably gives an accurate summary of the present state of our knowledge about the infraspecific taxonomy of the species. Although well differentiated from other species of *Trisetum*, it is an intricate complex variously split into arctic and boreal, high polypoid and low polypoid entities (Polunin, 1940; Hultén, 1959, 1968; Fernald, 1950). Further cytotaxonomic investigations may enable botanists to split up the complex but Jonsell *et al.* (1975) pointed out that knowledge of the chromosome numbers in this complex is highly incomplete and to infer the cytotype from morphological characters is not permissible except in restricted and well investigated areas.

Dore and McNeill (1980) consider *Trisetum spicatum* as circumpolar with a subsp. *spicatum* in eastern North America, known in Ontario only from Hudson Bay and James Bay. Our plant is treated by them under *T. triflorum* (Bigel.) A. &. D. Löve subsp. *triflorum*, which is disjunct with two general areas in Ontario, namely Hudson–James Bay and the north shore of Lake Superior.

Vaccinium uliginosum L. (Ericaceae)

DISTRIBUTION: Pigeon River to Michipicoten; Isle Royale; Michipicoten Island. Circumpolar low-arctic - mid-arctic - arctic (subarctic) - cordilleran. Maps: Porsild (1964), Hultén (1970), Young (1970), Soper & Heimburger (in press).

HABITAT: Rock pool herbfield (B.1. - B.3.), transitional herbfield/shrubbery (C.1.). In Arctic: acid soils on dry and wet sites, closed heath, sheltered sites especially solifluction slopes, snow patches and peaty marshes.

A polymorphic complex exhibiting several ploidy levels. Various authors have attempted to split the species with varying degrees of success. Young (1970) summarized previous work in conjunction with his own studies and concluded that plants occurring at Lake Superior are referable to the circumpolar low-arctic tetraploid subspecies: ssp. *pubescens* (Wormsk. ex Hornem.) Young.

Vaccinium vitis-idaea L. (Ericaceae)

DISTRIBUTION: From Grand Portage and Grand Marais, Minnesota, along the Lake Superior shore to Pic River; scattered through inland Minnesota (Cook County to Lake-of-the-Woods); Lake Nipigon and probably other lake shores and river banks north of Thunder Bay; Isle Royale (Smithwick Island), a collection made in 1868, (E.G. Voss, pers. comm., 1973). Circumpolar low-arctic - subarctic (mid-arctic) - cordilleran. Maps: Porsild (1964), Hultén (1970), Soper & Heimburger (in press).

HABITAT: *Empetrum* rock heath (A.4.), *Calamagrostis-Ledum* rock pool herbfield/shrubbery (B.3.) transitional herbfield/shrubbery (C.1.), bog herbfield/grassland/sedgeland (C.3.). In Arctic: acid, turfy sites, drier hummocks in bogs, and heath shrubbery.

Hultén (1970) recognized two subspecies, that at Lake Superior (ssp. *minus* (Lodd.) Hult.) being arctic-montane in distribution.

Woodsia alpina (Bolton) S.F. Gray (Polypodiaceae)

DISTRIBUTION: Scattered along the shore of Lake Superior from Temperance River to the Slate Islands; Michipicoten Harbour; Old Woman Bay; Dog Island, Orient Bay and Cooke Point in Lake Nipigon; Eagle Harbour on Keweenaw Peninsula; Marquette County, Michigan. Circumpolar low-arctic (high-arctic - subarctic). Maps: Hultén (1958), Porsild (1964), Soper & Maycock (1963).

HABITAT: Cliff herbfield (D.1.), generally where calcareous. In Arctic: rock crevices, cliffs, river ledges and scree slopes.

Woodsia glabella R. Br. (Polypodiceae)

DISTRIBUTION: Lake Superior shore from just south of Pigeon River to Pic River, extending inland to Thunder Bay and Lake Nipigon regions; Michipicoten Harbour south to Batchawana Bay, rarely inland; Grand Portage and Gooseberry River, Minnesota. Circumpolar mid-arctic - low-arctic (extreme-arctic - subarctic) cordilleran. Map: Hultén (1962).

HABITAT: Cliff herbfield (D.1.), probably always on calcareous sites. In Arctic: shaded talus and cliffs, in extreme north persisting on rocks not snow covered in winter although sometimes preferring sheltered crevices.

Appendix B. SHORELINE SAMPLING SITES FOR VEGETATION ANALYSIS

1. Mamainse Point (47° 02′ N, 84° 47′ W): shoreline adjacent to point, facing W (186 m.s.m)
2. McDonalds Islands (48° 43′ N, 86° 35′ W): shore of easternmost island in group (186 m.s.m)
3. Pic Island (48° 42′ N, 86° 36′ W): southeast tip near Allouez Is., shore facing SW (188 m.s.m)
4. Pic Island (48° 42′ N, 86° 36′ W): southeast tip near Allouez Is., level shore platform (188 m.s.m)
5. Pic Island (48° 42′ N, 86° 36′ W): southeast tip near Allouez Is., shoreline facing N (188 m.s.m)
6. Pic Island (48° 42′ N, 86° 36′ W): northeast corner, on north side of narrow promontory, facing N (185 m.s.m)
7. Pic Island (48° 43′ N, 86° 37′ W): northeast tip on narrow promontory, level shore platform (188 m.s.m.)
8. Spar Island (48° 41′ N, 86° 56′ W): shoreline on north side, facing NE (186 m.s.m)
9. Leadman Island (48° 41′ N, 86° 56′ W): southeast point, shore facing SE (190 m.s.m)
10. Leadman Island (48° 41′ N, 86° 56′ W): islet off southeast coast, whole shore (186 m.s.m)
11. Patterson Island (48° 40′ N, 86° 59′ W): near east end of Mortimer Channel, cliff facing N (186 m.s.m)
12. Patterson Island (48° 39′ N, 87° 02′ W): point opposite Edmonds Is., steep shore facing W (188 m.s.m)
13. François Island (48° 41′ N, 86° 59′ W): shoreline of whole islet (186 m.s.m)
14. Delaute Island (48° 42′ N, 86° 59′ W): small island off east side of island (186 m.s.m)
15. Delaute Island (48° 42′ N, 86° 59′ W): northeast corner, coastal platform facing NE (188 m.s.m)
16. Delaute Island (48° 42′ N, 86° 59′ W): northeast corner, shore platforms facing NE (188 m.s.m)
17. Delaute Island (48° 42′ N, 86° 59′ W): northwest corner of island, shore facing NE (186 m.s.m)
18. Delaute Island (48° 42′ N, 86° 59′ W): east of northeast point, shore facing N (188 m.s.m)
19. Mortimer Island (48° 41′ N, 86° 59′ W): east end of Mortimer Channel, cliff facing S (186 m.s.m)
20. Mortimer Island (48° 41′ N, 86° 59′ W): east end of Mortimer Channel, cliff facing S (186-190 m.s.m)
21. Islet (unnamed) between Edmonds Island and William Point, Mortimer Island (48° 39′ N, 87° 02′ W): whole shore (186 m.s.m)
22. Mortimer Island (48° 41′ N, 87° 01′ W): south coast near beacon, talus facing S (195 m.s.m)
23. Mortimer Island (48° 40′ N, 87° 04′ W): Barnard Point, at rear of beach, facing W (186 m.s.m)
24. Mortimer Island (48° 40′ N, 87° 04′ W): Barnard Point, shore at inlet, facing W (186 m.s.m)
25. Mortimer Island (48° 40′ N, 87° 04′ W): Barnard Point, damp cliff, facing N (186 m.s.m)
26. Mortimer Island (48° 40′ N, 87° 04′ W): 1.6 km E of Barnard Point, shore facing S (198 m.s.m)
27. Fluor Island (48° 39′ N, 88° 07′ W): west side, 3 km N of Starke Point, cliff facing W (186-215 m.s.m)
28. Fluor Island (48° 39′ N, 88° 06′ W): west side, 3.2 km N of Starke Point, talus facing W (198 m.s.m)
29. Moss Island (48° 39′ N, 88° 08′ W): east side, ca. 0.8 km south of site no. 30 (188 m.s.m)
30. Moss Island (48° 39′ N, 88° 08′ W): northern tip, on eastern side, shore facing E (190 m.s.m)
31. Moss Island (48° 39′ N, 88° 08′ W): northern tip, on western side, shore facing NW (188 m.s.m)
32. Agate Point (48° 36′ N, 88° 12′ W): east side of point, shore facing E (188 m.s.m)
33. Hawk Island (48° 35′ N, 88° 13′ W): south side, cliff facing S, near shore (186-195 m.s.m)
34. Marcil Bay (48° 35′ N, 88° 17′ W): entrance to bay on shore facing SW (186 m.s.m)
35. Marcil Bay (48° 35′ N, 88° 17′ W): entrance to bay on shore facing E (190 m.s.m)
36. Marcil Bay (48° 35′ N, 88° 17′ W): entrance on north side, shore facing SE (198 m.s.m)
37. Shesheeb Point (48° 35′ N, 88° 18′ W): more or less level coastal platforms (186 m.s.m)
38. Black's Wharf (48° 33′ N, 88° 19′ W): south end of peninsula, N of Lasher Island, shore facing E (185 m.s.m)
39. Black's Wharf (48° 33′ N, 88° 19′ W): south end of peninsula, N of Lasher Island, shore facing E (186 m.s.m)
40. Lasher Island (48° 31′ N, 88° 20′W): southeast side, shore facing SE (188 m.s.m)

41. Lasher Island (48° 31′ N, 88° 20′ W): southeast shore facing SE (194 m.s.m)

42. Lasher Island (48° 32′ N, 88° 20′ W): east side of island near north end, shore facing E (185 m.s.m)

43. Perley Island (48° 28′ N, 88° 22′ W): north side, shore facing NE (190 m.s.m)

44. Perley Island (48° 28′ N, 88° 22′ W): north end, shore facing N (190 m.s.m)

45. Perley Island (48° 28′ N, 88° 22′ W): north end, shore facing NE (190 m.s.m.)

46. Macoun Island (48° 28′ N, 88° 26′ W): islet off south end, level shoreline (186 m.s.m)

47. Porphyry Island (48° 21′ N, 88° 38′ W): point south of lighthouse, shore platform facing E (186 m.s.m)

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